UNIVERSITÉ DU QUÉBEC À MONTRÉAL

# LA PERFORMANCE DE LA LIVRÉE DES FORÊTS (*MALACOSOMA DISSTRIA* HBN.) DANS UN CONTEXTE DE MIGRATION ENTRE CLONES DE PEUPLIERS HYBRIDES (*POPULUS* SPP.) ET HÔTES NATURELS

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## RÉSUMÉ

Le déploiement des plantations de peupliers hybrides en milieu forestier les expose à un ensemble d'espèces d'insectes herbivores qui s'attaquent déjà aux arbres du genre *Populus*. La Livrée des forêts (*Malacosoma disstria* Hbn.) est un de ces insectes indigènes qui pourrait s'attaquer aux peupliers hybrides. La livrée étant généraliste dans ses habitudes alimentaires, les plantations de peupliers hybrides pourraient être attaquées tant en forêt boréale où le peuplier faux-tremble (*Populus tremuloides* Michx.) est abondant, qu'en forêt tempérée, où l'érable à sucre (*Acer saccharum* Marsh.) domine le paysage. Dans cette étude, la performance des larves de Livrée des forêts a donc été examinée sur ces hôtes naturels et sur les clones de peupliers hybrides recommandés pour les domaines bioclimatiques boréaux et tempérés du Québec. La performance a aussi été examinée lors de transferts des clones vers les hôtes naturels et des hôtes naturels vers les clones. Les clones recommandés pour le nord (hybridation entre *P. balsamifera* et *P. maximowiczii*) se sont avérés être résistants comparativement au peuplier faux-tremble. Les clones recommandés pour le sud (hybridation entre *P. deltoides* et *P. nigra*) ont montré une résistance intermédiaire entre le peuplier faux-tremble et l'érable à sucre. La résistance des clones était diminuée lorsque les larves de Livrée des forêts étaient transférées du peuplier faux-tremble vers les clones du nord ou du sud, mais ce ne sont pas toutes les variables de performance qui ont été affectées. Le dénominateur commun parmi toutes les réponses aux diètes était un allongement du temps de développement comparativement au meilleur hôte, le peuplier faux-tremble. Cette plasticité dans le temps de développement permet l'atteinte d'un poids minimal pour la pupaison. Une augmentation du temps de développement réduit la probabilité que les livrées s'étant alimentées sur les clones résistants se reproduisent avec celles s'étant nourrit de clones plus susceptibles, sur le peuplier faux-tremble et dans certains cas, avec des individus qui auront migré des peuplements naturels vers les plantations. Le risque de développer une contre-résistance pourrait augmenter sous ces conditions. Les stratégies de déploiement ont été discutées suite à ces résultats.



**Mots-clés :** Livrée des forêts, peuplier hybride, résistance, transfert de diète, poids critique

# INTRODUCTION GÉNÉRALE

## 0.1 Problématique

Un des corolaires de l'aménagement écosystémique dans les forêts publiques est l'intensification de la production de bois sur de petites superficies. Cette sylviculture intensive est notamment rendue possible grâce aux arbres à croissance rapide tels que les peupliers hybrides (*Populus* spp.) qui, en plantation, permettent la récolte d'une grande quantité de bois sur une courte rotation et un petit territoire (Fortier, 2008). Outre pour leur croissance rapide, le programme d'amélioration génétique du peuplier de la Direction de la recherche forestière du ministère des Ressources naturelles du Québec (DRF-MRN) sélectionne des clones de peupliers hybrides pour leur rusticité, la qualité de leur bois, leur rectitude ainsi que leur résistance aux pathogènes (Réseau ligniculture Québec, 2011). Par contre, en ce qui a trait à la résistance des peupliers hybrides aux insectes, elle n'est pas encore considérée systématiquement dans la sélection des clones de peupliers hybrides.

Les espèces du genre *Populus* genus sont attaqués par de nombreuses espèces de pathogènes et d'insectes (Tillesse et al., 2007). Ils sont les hôtes d'environ 770 espèces d'insectes en Amérique du Nord. Au Canada, la Livrée des forêts a été identifiée comme étant un risque majeur pour les plantations de peupliers hybrides (Volney et al., 2005).

La Livrée des forêts (*Malacosoma disstria* Hbn.), un important défoliateur des peupliers naturels et d'autres feuillus, est endémique à toutes les régions du Québec méridional (sous le 49e degré de latitude) où l'on retrouve les plantations de peupliers hybrides (Cooke et Lorenzetti, 2006). Dans le sud de la province, elle s'attaque surtout aux érables à sucre (*Acer saccharum* Marsh.), car cette espèce est dominante

dans le paysage, alors que plus au nord, elle s'attaque plutôt au peuplier faux-tremble (*P. tremuloides* Michx.) qui est l'espèce feuillue qui domine dans ces régions. Les épidémies de Livrée des forêts pourraient s'étendre dans les plantations de peupliers hybrides suite à une migration des larves pour s'alimenter ou encore par la ponte des femelles directement sur ces peupliers hybrides.

Historiquement, les épidémies de Livrée des forêts ont été récurrentes aux 9 ans en Abitibi-Témiscamingue et aux 13 ans en Estrie (Cooke et Lorenzetti, 2006). Au Québec, la durée des infestations est en moyenne de 2.6 ans dans les régions où les épidémies sont cycliques (Cooke et al., 2009). Considérant la durée des cycles épidémiques de la livrée dans le nord et le sud du Québec et qu'une rotation chez les peupliers hybrides est généralement de 20 ans (Réseau ligniculture Québec, 2011), il pourrait théoriquement y avoir deux épidémies dans les plantations dans les régions plus au nord et une dans les régions du sud au cours d'une rotation. Une forte défoliation par la Livrée des forêts peut causer une importante réduction de la croissance radiale des peupliers faux-tremble (Cooke et Roland, 2007; Froelich et al., 1955). De plus, la mortalité des peupliers faux-tremble est fonction du nombre d'années consécutives de défoliation (Churchill et al., 1964; Moulinier et al., 2011). A cause des effets cumulatifs des défoliations consécutives, les effets sur les plantations seraient probablement moindres dans le cas où les épidémies débuteraient sur les hôtes naturels pour ensuite migrer vers les plantations en cours de cycle. Par contre, si la Livrée des forêts pond dès l'initiation d'un cycle épidémique dans les plantations de peupliers hybrides, les effets sur la croissance et la mortalité des arbres pourraient être plus importants.

Mis à part les travaux réalisés au sein du Consortium de recherche sur les insectes forestiers (iFor) qui ont porté sur la préférence de la livrée en laboratoire envers différents clones de peupliers hybrides (Ralph, 2012; Rajalingham et al., 2011), il n'existe aucune étude sur le développement larvaire de la Livrée des forêts sur les

clones spécifiques au Québec pour lesquels une prise alimentaire a pu être démontrée. Les connaissances sur les facteurs chimiques de résistance des peupliers hybrides sont aussi peu nombreuses en général (Robison & Raffa, 1994, 1997) et inexistantes pour les clones spécifiques au Québec. En revanche, les espèces parentes américaines utilisées pour les croisements au Québec (*P. deltoïdes*, *P. balsamifera* et *P. trichocarpa*) sont toutes des hôtes, à divers degrés, des espèces du genre *Malacosoma* auquel appartient la Livrée des forêts (Burns & Honkala, 1990).

Dans un contexte écologique, le changement d'hôte entre les clones de peupliers hybrides et les hôtes naturels dominants dans chaque région est à considérer. Une modification du développement larvaire, soit au niveau de la fécondité (qui peut être inférée à partir du poids des pupes femelles) ou encore un effet sur la survie, pourrait influencer la dynamique épidémique. Une évaluation de la composition des feuilles en eau et en azote des différents hôtes pourrait amener des explications sommaires sur les différences développementales des larves sur chacun des hôtes. En effet, bien que les insectes qui s'attaquent aux peupliers sont affectés dans leur développement par les phénols glycosidiques produits par ces espèces forestières, les variations interclonales en azote chez ces hôtes se sont également avérées très importantes (Lindroth et al., 1987; Osier et al., 2000a,b).

## 0.2 État des connaissances

### 0.2.1 Peupliers hybrides

Au Québec, le MRNQ a développé une quarantaine de clones adaptés pour les différentes régions et sous-régions écologiques (Périnet et al., 2007). Pour le sud du Québec, ce sont surtout les clones issus du croisement entre *P. deltoides* et *P. nigra*

qui sont les mieux adaptés, tandis que pour le nord du Québec, ce sont les croisements entre *P. balsamifera* et *P. maximowiczii* qui dominent.

Les deux seules études qui ont concerné la performance de la Livrée des forêts sur des peupliers hybrides (Robison et Raffa, 1997, 1994) portaient sur des clones et des croisements différents de ceux utilisés au Québec. Il est donc difficile de faire des prédictions spécifiques sur la performance des larves de Livrée des forêts sur les différents clones de peupliers hybrides recommandés au Québec. Par contre, certaines études démontrent une plus grande résistance aux insectes chez les clones de peupliers hybrides contenant *P. maximowiczii* (Broberg et Borden, 2005; Kruse et Raffa, 1996; Ramírez et al., 2004; Robison et Raffa, 1994).

### 0.2.2 Contenus en eau et en azote des feuilles

L'azote est un élément essentiel à la croissance des organismes étant donné qu'il est un important constituant des protéines (Mattson, 1980). Une diète faible en protéines et par le fait même en azote, limite en effet la croissance des larves de la livrée (Colasurdo et al., 2009). Selon Hemming et Lindroth (1995), il y aurait une corrélation positive entre la concentration en azote et le poids des pupes. Il y aurait aussi une corrélation positive entre la performance des larves et le contenu en eau des feuilles (Scriber & Slansky, 1981). Par contre, les contenus en eau et en azote co-varient dans le temps à l'échelle de l'arbre, de même qu'avec certains composés secondaires (Mattson & Scriber, 1987). Ainsi, il est difficile de présumer d'une relation de cause à effet entre la performance des larves et le contenu en eau.

### 0.2.3 Livrée des forêts

Les larves de Livrée des forêts émergent au début du printemps, généralement en synchronie avec le débourrement de leur hôte primaire. Le cycle larvaire s'étire jusqu'au milieu de l'été en passant par généralement 5 à 6 stades. Elles passeront 10 à 15 jours sous forme de chrysalides à l'intérieur d'un cocon. Une fois adulte, la Livrée des forêts ne s'alimente pas, elle s'accouple et meurt après quelques jours (Fitzgerald, 1995). Une seule masse d'œufs est produite par femelle, contenant entre 80 et 480 œufs (Witter et Kulman, 1969). Les Livrées des forêts passent l'hiver sous forme de larves pharates (Fitzgerald, 1995). Lors des épidémies, si la nourriture vient à manquer, elles migreront vers de nouveaux arbres. Ceci se fait surtout au $4^{e}$ et $5^{e}$ stade larvaire, stades auxquels la prise de nourriture est plus importante (MRNQ, 2013).

### 0.2.4 Développement larvaire

La performance des larves peut être évaluée par le poids de la chrysalide, notamment chez un insecte qui ne se nourrit pas à l'état adulte et dont les réserves accumulées durant la vie larvaire vont déterminer la fécondité (Fitzgerald, 1995 ; Colasurdo et al., 2009). Les espèces d'insectes qui ont évolué vers cette stratégie sont référées comme des *capital-breeders* dans la littérature scientifique anglophone. Ainsi, chez cette catégorie d'insectes, le poids des femelles est corrélé fortement et positivement avec leur fécondité (Honek, 1993). Une bonne performance larvaire peut aussi être représentée par un court temps de développement, ce qui aura pour effet de diminuer la susceptibilité des larves aux ennemies naturels (Parry et al., 1998). La performance des larves est particulièrement influencée par l'alimentation de celles-ci. La qualité, et

donc la composition en eau et en azote de l'hôte sur lequel elles s'alimentent, est déterminante.

Malgré le fait que le peuplier faux-tremble et l'érable à sucre soient les hôtes naturels de la Livrée des forêts, ses performances larvaires sont meilleures sur le peuplier faux-tremble que sur l'érable à sucre. En effet, le temps de développement des larves est plus long lorsqu'elles s'alimentent sur l'érable à sucre et la masse pupale est plus faible (Lorenzetti et al., 1999; Trudeau et al., 2010).

La qualité de la diète durant les premiers stades larvaires est un facteur particulièrement important dans la performance globale du développement larvaire (Zalucki et al., 2002) et ceci est particulièrement bien démontré par les études sur la synchronisation entre le début de l'alimentation et le débourrement des hôtes (Van Asch & Visser, 2007). Par exemple, une mauvaise synchronisation chez la livrée entraîne une prolongation de la période larvaire et parfois l'ajout de stades, de même qu'une faible masse pupale ainsi qu'un plus haut taux de mortalité (Jones et Despland, 2006).

En ce qui a trait aux études sur les changements d'hôtes au cours du développement larvaire, une tendance ressort concernant l'importance de l'hôte consommé et du moment auquel l'hôte est consommé durant le cycle larvaire (Hwang et al., 2007; Stoyenoff et al., 1994a,b) : l'hôte consommé en début de développement s'avère d'une grande influence sur la performance globale. Ceci est dû aux différences dans la qualité nutritionnelle et le contenu en métabolites secondaires selon l'âge des feuilles ainsi que la sensibilité des larves selon leur stade à ces variations phénologiques dans la diète.

**Le concept de résistance**

Le concept de résistance aux insectes est utilisé autant en foresterie[1] qu'en agriculture. La résistance est définie comme la capacité d'une plante à limiter les dommages fait par les insectes ainsi qu'à diminuer son intérêt comme plante hôte pour ces insectes (Painter, 1951). Cette capacité de la plante est exprimée par des traits fonctionnels qui peuvent être autant physiques que chimiques. La présence de poils, d'épines ou encore de toxines peuvent conférer une résistance à la plante face aux insectes. De plus, la résistance est considérée comme relative, c'est-à-dire que pour statuer qu'un arbre est résistant à une espèce d'insecte, il faut le comparer à un autre arbre sur lequel on observe des dommages plus importants causés par ces mêmes insectes (Owens, 1975).

Ceci dit, la résistance peut aussi être évaluée au niveau des conséquences qu'elle a sur les insectes (Beck, 1965). D'ailleurs, l'une des trois catégories de résistance des plantes aux insectes selon Painter (1951), soit l'antibiose, implique nécessairement la mesure des effets délétères sur l'une ou l'autre des variables de performance suite à l'alimentation. Plus récemment, Larson (2002), traitant de la résistance des arbres aux insectes en relation avec leur longévité plus grande que celle des plantes agricoles, abonde dans le sens de Beck (1965). Sur un hôte hautement favorable, les insectes se développement rapidement, atteignent un poids élevé, ont un haut taux de fécondité et ont un faible taux de mortalité. À l'inverse, les insectes utilisant un hôte résistant auront une plus faible performance, soit un développement ralenti, un faible taux de fécondité, un taux de mortalité plus élevé, ou une combinaison de ces réponses. Dans ce mémoire, la résistance des clones de peupliers hybrides sera mesurée selon la performance de la Livrée des forêts sur ceux-ci relativement à sa performance sur ses hôtes naturels, le peuplier faux-tremble et l'érable à sucre.

[1] Le concept de résistance, bien que développé initialement dans un contexte d'amélioration des végétaux utilisés en agriculture, est toujours d'actualité en sciences forestières, de même que l'utilisation de cette terminologie. Par exemple, un important congrès international sur la résistance des arbres s'est tenu en 2011, à Eugène, en Orégon : The Fourth International Workshop on the Genetics of Host-Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees (http://www.fs.fed.us/psw/publications/documents/psw_gtr240/).

## 0.3 Hypothèses

La meilleure performance de la Livrée des forêts sur le peuplier faux-tremble que sur l'érable à sucre n'étant plus à démontrer (Lorenzetti et al. 1999; Trudeau et al., 2010), aucune hypothèse à ce niveau ne sera formulée. D'autre part, l'objectif de cette étude n'étant pas d'examiner la performance de l'insecte sur les différents clones, mais bien entre les clones et les hôtes naturels, aucune hypothèse n'est avancée au niveau des variations clonales dans la résistance à la livrée. Ceci dit, on s'attend à une résistance à la Livrée des forêts plus importante chez les clones du nord considérant les espèces parentes utilisées. Les clones contenant le parent *P. maximowiczii* montrent une plus grande résistance à la Livrée des forêts (Robison et Raffa, 1994) et à d'autres insectes (Broberg et Borden, 2005; Kruse et Raffa, 1996; Ramírez et al., 2004). De plus, les clones contenant *P. balsamifera* dans l'étude de Robison et Raffa (1994) montrent aussi une certaine résistance contre la livrée. Chez les clones du sud, *P. deltoides* est un hôte naturel de la livrée (Morris et al., 1975) tandis que pour *P. nigra*, aucune résistance particulière à la livrée n'a été déterminée.

Dans cette étude, il est apparu utile de formuler des hypothèses qui, si elles sont confirmées, permettraient d'anticiper les réponses de la Livrée des forêts dans un contexte où les plantations de peupliers hybrides se retrouvent dans une matrice

d'hôtes naturels. Considérant l'importance de la diète pour les premiers stades larvaires et la plus grande capacité des larves plus âgées de la livrée à migrer d'un hôte à l'autre, deux hypothèses générales sont formulées

- Hypothèse 1: La performance des larves ayant fait un changement de diète au cours de leur développement sera similaire si la performance sur le clone est de valeur égale à celle observée sur l'hôte naturel alors qu'elle sera intermédiaire aux performances sur le clone et l'hôte naturel si elles différent sur ces hôtes.
- Hypothèse 2: Les larves s'étant alimentées de l'hôte de qualité supérieure durant les premiers stades larvaires seront plus performantes que celles ayant fait le changement de diète dans le sens inverse.

Enfin, il est attendu de façon générale que la performance larvaire soit meilleure sur les diètes contenant un taux élevé d'azote et un contenu élevé en eau.

CHAPITRE I

# DEPLOYMENT OF HYBRID POPLAR PLANTATIONS ON CLEARED FOREST LAND: LESSONS FROM A CAPITAL BREEDER INSECT FOLIVORE WITH PLASTIC DEVELOPMENT TIME

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## 1.1 Abstract

Deploying hybrid poplar plantations on cleared forest land expose them to a suite of insect herbivores which can have tree species from the natural forest matrix and *Populus* Spp. as shared hosts. The most ubiquitous defoliator in North America is the forest tent caterpillar (FTC; *Malacosoma disstria* Hbn.). This native insect feeds on most deciduous trees species, especially on quaking aspen (*Populus tremuloides* Michx.) and on sugar maple (*Acer saccharum* Marsh.). In this study, the performance of FTC larvae was examined on both these natural hosts and on clones recommended for Quebec's bioclimatic domains in which the natural hosts are the dominant deciduous species. Performance was also examined in experiments where FTC larvae switched from clone to natural hosts and from the latter to the former. Northern recommended clones (hybridizations between *P. balsamifera* and *P. maximowiczii*) were found to be relatively resistant compared to aspen. Southern recommended clones (hybridizations between *P. deltoides* and *P. nigra*) expressed intermediate resistance relative to aspen and sugar maple. Clone resistance was reduced when FTC larvae switched from aspen to northern or to southern clones, but not all performance variables were affected. They had lower pupal weight compared to aspen but took less time to reach pupation and had better survival than when fed only on clones. The one common denominator across all feeding treatments was extended development time compared to the preferred host, aspen. This plasticity in development time allows FTC larvae to reach a minimal size at pupation. However, the FTC is a capital breeder; hence its window of opportunity for reproduction is very short. An increase in development time thus reduces the likelihood of FTC that fed on resistant clones of reproducing with individuals that fed on more susceptible clones, on aspen, and even in some cases with individuals that would have migrated from natural stands to plantations. The risk of counter-resistance development is expected to increase under these conditions. Deployment strategies are discussed in light of these results.

**Keywords:** forest tent caterpillar, hybrid poplar, host switching, critical size, fast growing trees

## 1.2 Introduction

Fast-growing tree plantations have been steadily increasing in many countries during the last decade. In addition to the traditional uses of poplars for timber, bioenergy production, and environmental protection (windbreak, soil erosion and phytoremediation), hybrid poplar (*Populus* spp.) plantations are efficient solutions for carbon sequestration (FAO, 2012). In 2012, the total area of planted poplars worldwide reached 8.6 million ha with close to 90% found in China alone (FAO, 2012). In Europe, poplar plantations extend over more than 800 thousand ha. In Canada and in the United States, fast-growing tree plantations are still modest with some 45 thousand ha in 2012, but they are found in many provinces (Larocque et al., 2013) and states (Berguson et al., 2010). In Quebec, poplar cultivation greatly increased in the 2000's to reach 1 to 1.5 million of hybrid poplar trees delivered every year by the Ministry of Natural Resources (Derbowka, 2012). Since the beginning of the poplar improvement program at the Ministry in 1969, more than 5,000 clones have been evaluated, and over 40 different clones have been released for use in plantations (Périnet et al., 2007). The great majority of these trees are planted on cleared forest land in Quebec.

Trees in *Populus* genus are attacked by numerous pathogens and insects (Tillesse et al., 2007). They are hosts to some 750 species of insects in North America. Hybrid poplar plantations in Canada are presently a small addition to the 30.3 million ha of native poplars and aspens already present in natural forests, the largest *Populus* area in the world (FAO, 2012). Hybrid poplar plantations in Minnesota, USA, are part of a landscape where quaking aspen (*Populus tremuloides* Michx.) dominates over 2.5 million ha and sugar maple (*Acer saccharum* Marsh.) and other deciduous trees over 1.5 million ha (Miles et al., 2002). In Quebec, hybrid poplar clones have been developed for the different bioclimatic domains (Périnet, 2007): from the quacking

aspen-dominated landscapes of the boreal forest to the sugar maple-dominated landscapes of the temperate deciduous forest. The most ubiquitous indigenous defoliator to occur in the majority of the areas of North America where hybrid poplar plantations are located is the forest tent caterpillar (FTC; *Malacosoma disstria* Hbn.). Outbreaks by this insect can extend over millions of hectares. In the past forty years, there has been an on-going outbreak 70 to 97 % of the time in Alberta, Ontario and Quebec (National forestry database, 2013). Minnesota forests have been hosts to eleven FTC outbreaks in the last 120 years (Minnesota Department of Natural Resources, 2013). An analysis of the FTC historical defoliation records (1938-2002) for Quebec indicated that outbreaks occur cyclically every 9 years in the northwest region dominated by quaking aspen, and every 13 years in the south where sugar maple dominates (Cooke and Lorenzetti, 2006). Defoliation by the FTC causes important radial growth reductions (Barter and Cameron, 1955; Cooke and Roland, 2007; Duncan and Hodson, 1958; Froelich et al., 1955; Hogg, 1999; Pollard, 1972; Witter, 1979) and mortality (Churchill et al., 1964; Man and Rice, 2010; Moulinier et al., 2011; Reinikainen et al., 2012) in quaking aspen and in sugar maple (Bauce and Allen, 1991; Hartmann and Messier, 2008; Wood et al., 2009).

In Canada, FTC has been identified as one of the major threats to hybrid poplar plantations (Volney et al., 2005). Considering the ubiquity of the FTC in North American landscapes, its outbreak status recurrence in many areas, and the risk this insect poses to hybrid poplar plantations, it is rather surprising that relatively little attention has been given to the FTC-hybrid poplar interaction (Constabel et al., 2000; Robison and Raffa, 1997, 1994; Wang and Constabel, 2004). In the present study, a holistic approach to this interaction has been adopted. The presence of quaking aspen and sugar maple in the forest cover and the ontogenic behavior shift of the FTC to migrate during the later stages of its larval life (Despland and Hamzeh, 2004) emphasize the importance of studying hybrid poplar clones in the context of its deployment environment. During the peak years of FTC outbreaks, we expect that

clone resistance will likely not be enough to prevent defoliation by this insect. FTC is well known to defoliate many other species when preferred hosts have been consumed during phases of high density populations (Hodson, 1941; Stehr and Cook, 1968). Indeed, late instar larvae have been seen to feed on white spruce under such conditions (*F. Lorenzetti, personal observations*), and even on the usually completely avoided red maple (Nicol et al., 1997; Wink and Allen, 2007). However, it can be anticipated that as the areas planted with hybrid poplar clones increase in size within the forest matrix, endemic FTC populations will be present in those plantations and migrations of larvae from natural forests will occur. For such short-rotation plantations, every year without defoliation, even light to moderate, is a gain towards the benefits of high-yield expected from them. It would thus be of considerable advantage to know beforehand the responses of FTC larvae in the context of plantations imbedded in a forest matrix in which the insect is already present. Considering the low number of studies on FTC on hybrid poplars, it is important to know which performance variables (survival, development time and pupal weight/fecundity) are the most affected to understand the likely dynamics of this insects in plantations. This information is also critical to support the design of deployment strategies that minimize the risk of development of counter-resistance in the insect.

In the present study, the performance of FTC larvae was examined on hybrid poplar clones developed and recommended by the Quebec Ministry of Natural Resources for the north (aspen-dominated) and for the south (sugar maple-dominated) of the province. The relative resistance of these clones towards FTC was compared to larval performances observed on the insect's natural hosts and when switching from the selected clones to the natural hosts, and when switching from the natural hosts to the selected clones. The results presented here are applicable in other areas where hybrid poplar plantations are being developed and eruptive species of defoliators are part of the landscape.

## 1.3 Methods

### 1.3.1 Hybrid poplars, natural host trees and leaf sampling

Hybrid poplar material were from a common plantation established in 2008, either from bare-rooted plants (clones of the northern experiment) or from cuttings (clones of the southern experiment), in Ripon, Quebec, Canada. Plant material was provided by the Direction de la recherche forestière of the Quebec Ministry of Natural Resources. The location of the plantation (45.78331 N, -75.08780 W) is at the transition between the sugar maple-basswood and the sugar maple-yellow birch bioclimatic domains (Saucier *et al.*, 2011), thus at the limit between the northern and southern zones for hybrid poplar deployment in Quebec, as depicted on the map in Figure 1.1. The mean annual temperature at the closest station (13 km) is 3.9°C and the mean annual precipitation is 1105.3 mm (climate normals 1971-2000; Environment Canada, 2013). The trees were aged 4-5 years at the time of the experiments. Leaf material of the natural hosts of the FTC, quacking aspen and sugar maple, were from trees growing in natural stands also located in Ripon. The aspen stand was composed of 10-20 years old trees and the sugar maple stand was composed of ca. 70 years old mature trees.

Three hybrid poplar clones recommended for the north of the province of Quebec were used for the northern experiment. These clones (hereafter denoted BM1, BM2 and MB3) are all from hybridizations between *P. balsamifera* and *P. maximowiczii* (BxM for the two firsts and MxB for the last one, the first letter indicating female parentage). Three hybrid poplar clones (DN1, DN2 and DN3) recommended for the south of the province of Quebec were used for the southern experiment, each from hybridizations between *P. deltoides* and *P. nigra* (DxN). Clone selection was based on the capacity of FTC larvae to feed on the leaves of the selected clones (Ralph,

2012), on the frequency of use of these clones in plantations from recent years, as well as on their suitability to be planted across several Quebec bioclimatic domains (Fig.1).

Leaf material to feed the FTC larvae in the Ripon laboratory was collected at the edge of selected trees to avoid light limited leaves. Selected trees were all vigorous with green and healthy leaves. Leaves were collected in the morning about every two to three days, or as soon as they were no longer turgescent in the laboratory or entirely consumed. Collected leaves were maintained in florist vials filled with distilled water. At each collection, leaves were collected from sets of different trees to minimize possible induction of plant defenses. Throughout the experiments, except at leaf flush, leaves of intermediate phenological age were selected from the clones and from aspen to minimize differences in phenology among hosts. However, in the case of sugar maple, which has determinate growth, leaves increased in maturity with time.

### 1.3.2 Insect material, rearings and host switching

FTC egg masses used for the southern experiment were collected on sugar maple from outbreak populations in southern Ontario and were obtained from the Canadian Forest Service Great Lakes Forestry Centre in Sault Ste. Marie, Ontario. Egg masses for the northern experiment were produced by insects of the same origin but reared on aspen for one cycle in the Ripon laboratory. Egg masses were stored at 0 ± 2°C until needed. Before they were transferred at 21 ± 1°C for hatching, the spumaline that covers the egg masses was removed with a razor blade and egg masses were surface-sterilized with a solution of 4 % sodium hypochlorite to destroy a maximum of pathogens (Grisdale, 1985). Rearings were synchronised to start with leaf bud break on the different hosts. FTC larvae were reared in 1 L cylindrical plastic containers

with a fine-mesh net fitted on the lid. Throughout the experiments, from egg hatch to the completion of the pupal stage, the containers were kept in a controlled environment chamber (16h:8h L:D, 20-22°C and 70-100% RH). Each container initially received 20 larvae that hatched on the same day and constituted a replicate on a given host, or in a host switching treatment. There were three replicates per host/host switching treatment for the southern experiment and four for the northern experiment. To ensure genetic mixing in each replicate, larvae were selected from different egg masses. Larvae were fed *ad libitum*. Host switching occurred when more than 50 % of larvae in a replicate reached the fourth instar. Due to an insufficient number of larvae synchronously hatching at the onset of the southern experiment, one switching treatment (DN2 to aspen) was not implemented. In total, the northern experiment involved ten treatments (40 replicates and 800 larvae) and the southern experiment, sixteen (48 replicates and 960 larvae).

### 1.3.3 Larval performance

Survival was recorded at 1 to 3 days intervals. Molt dates were noted when more than 50 % of larvae molted to the next instar. For the northern experiment, larvae were group-weighed at each molt in each replicate. Time to pupation was measured from egg hatch to pupation. Twenty-four hours after pupation, each pupa was weighed and the sex was determined. Moth emergences were recorded to determine the duration of the pupal stage.

### 1.3.4 Water and nitrogen content of the foliage

At each larval molt in each treatment, fresh leaves were collected for water and nitrogen content determination from the same trees used to feed the FTC larvae. For hybrid poplar clones in the southern experiment, for which the trees were smaller, eight replicates composed of the pooled leaf material from four different trees were completed at each sampling date. For the northern experiment, each of the eight replicates was formed with the leaf material of only one tree, because the trees were larger. In the same way, six replicates, each composed of leaf material from the same six pairs of aspen trees, were completed at each sampling date, whereas six replicates were formed with the leaf material from six sugar maple trees. Three grams (fresh weight) of leaves per replicate were collected at each sampling date. Sampling was conducted in the morning and the material was put on ice immediately. The leaves were weighted without the petiole in the laboratory and samples were kept at -20°C until analyses. Samples were freeze-dried and then weighed. Water content was determined at this moment. Dry leaves were grinded to a fine powder using a coffee bean grinder prior to extraction. Nitrogen (N) was extracted by sulfuric acid digestion (Dolgin et al., 2005) and then analyzed on a flow injection analyser (QuikChem 8500, Lachat Instruments, Loveland, CO, USA) using the QuikChem method # 13-107-06-2-D (Diamond, 1996).

### 1.3.5 Statistical analyses

To determine whether there were significant differences in larval performance between feeding treatments (natural host, natural host to poplar clones, clones to natural host and clones), multivariate analyses of variance (MANOVAs) were conducted for each sex separately using pupal weight, time to pupation and survival

rate as independent variables. MANOVAs were followed by canonical discriminant analyses to determine which treatments were different, based on the nonoverlap of 95% confidence regions, and which independent variable influenced the observed differences the most. Non-linear regression analyses (power-curve fitting) were performed on the larval or pupal weight relationships with time to reach a given instar or pupation. To determine if mortality was more important before or after host switching occurred, non-parametric paired tests (Wilcoxon signed-rank test) were performed. For MANOVAs, canonical discriminant analysis and Wilcoxon signed-rank test, clones were grouped by experiment. To determine whether there were significant differences in the duration of the pupal stage between feeding treatments, one-factor analyses of variance (ANOVAs) were conducted for each sex and experiments (northern and southern) separately.

Relationships between insect performance (pupal weight and time to pupation) and foliar water and nitrogen contents of hosts were assessed using multiple regressions. Foliar water and nitrogen contents were first averaged using the weighted means between foliage collection dates. Average contents were then computed for the total duration of the larval stages, of the larval stages before or after the fourth instar, and used as independent variables. The models with the higher $R^2$ are presented.

Analyses of covariance (ANCOVAs) were performed to test (1) if there were differences in larval growth models among feeding treatments, i.e., the relationship between the difference in larval size at the onset of the ultimate instar and an estimated threshold size to pupate (DiffSize) and larval growth trajectories (GR), calculated as the observed growth rates during the 4th through the penultimate instar, and (2) the relationship between pupal weight and DiffSize.

Before performing analyses on larval performance or before using the foliar water and nitrogen content data, observed values that differed more than 99% from the

mean (i.e. more than 2.57 times the standard deviation) were removed (outlier detection performed within replicates for performance data and between replicates for foliar water and nitrogen content data). All statistical analyses were conducted using the JMP 10 statistical software package (SAS Institute, Cary, NC, USA) except for canonical discriminant analyses which were conducted using the "candisc" package (Friendly and Fox, 2013) running on the R statistical freeware platform (version 2.15.2; R Development Core Team, 2012), and for ANCOVAs which were ran in NCSS (NCSS, version 2004, Kaysville, Utah, USA).

## 1.4 Results

### 1.4.1 Time and survivorship to, and weight at, pupation

The relationships between pupal weight and time to pupation were well-represented by highly significant (*P-values* of <0.0001) negative power-law curves for FTC larvae reared on the foliage from natural hosts and hybrid poplar clones in both the northern and southern experiments, and for both sexes (Fig. 2). The coefficients of determination ($R^2$) for these models were 0.76 (females) and 0.43 (males) for the northern experiment, and 0.84 (females) and 0.71 (males) for the southern experiment. The slopes of the power-law curves were steeper for females than for males, and for the southern experiment (females: -0.916; males: -0.731) than for the northern experiment (females: -0.468; males: -0.273). A steeper slope is indicative that the insects were unable to increase their weight by increasing their development time. A slope of -1 results in a reduction of 50% of the predicted pupal weight if development time is doubled from 30 days, whereas a slope of -0.25 results in a reduction of 15.9% of the predicted pupal weight. The negative relationships between pupal weight and time to pupation no longer hold, i.e. the slopes are not significantly

different form zero, if the performance of larvae from the host switching treatments are included in the models (*results not shown*). Consequently, the $R^2$ of the models including the host switching treatments were greatly reduced: by 94.7 % for the females and by 97.7 % for the males in the northern experiments, and by 57.1 % for the females and by 70.4 % for the males in the southern experiment. These results suggest a more complex adjustment of weight gain during larval development when host switching occur. Indeed, in both the northern and southern experiments, larvae switching from aspen to clones (*solid line green box in* Fig. 2) had generally shorter development time than larvae switching from clones to aspen (*dotted line green box in* Fig. 2), but also generally had lowered pupal weight. In the southern experiment, larvae switching from sugar maple to clones (*solid line red box in* Fig. 2) or from clones to sugar maple (*dotted line red box in* Fig. 2) generally pupated within the same time frame, but they tended to reach larger pupal weight when they switched to sugar maple than when they switched to clones.

Multivariate analyses of variance (MANOVAs) revealed significant differences among feeding treatments with respect to FTC pupal weight, time to pupation and survival rate in all experiments. Canonical discriminant analyses further revealed between which feeding treatments the difference lied, and which independent variable contributed the most to these differences. MANOVAs revealed differences between feeding treatments for females and males in the northern experiment (Pillai's trace; $F_{6,62}$ = 28.25, $P$ = <0.0001; $F_{6,64}$ = 28.17, $P$ = <0.0001) and in the southern experiment with aspen (Pillai's trace; $F_{6,46}$ = 3.87, $P$ = 0.0033; $F_{6,46}$ = 4.26, $P$ = 0.0017) and with sugar maple (Pillai's trace; $F_{6,50}$ = 8.62, $P$ = <0.0001; $F_{6,50}$ = 5.10, $P$ = 0.0004) as the natural hosts. The canonical discriminant analyses (Fig. 3) showed the same patterns for females and males in each experiment. In the northern experiment, both time to pupation and survival rates – represented by symbol size in Figure 1.2, discriminated between larvae fed only aspen or switching from aspen to clones, from larvae fed only clones, or switching from clones to aspen. Larvae in the

first groups had greater survival rates and shorter development times than larvae in the second groups (Fig. 2 and 3). Pupal weights further discriminated within groups, with larvae fed clones, or switching from aspen to clones, having lower weights than larvae fed aspen or switching from clones to aspen. In the southern experiment with aspen as the natural host, time to pupation, but not survival rates, discriminated between larvae fed only aspen or switching from aspen to clones, from larvae fed only clones, or switching from clones to aspen. As for the northern experiment, larvae in the first groups had shorter development times than larvae in the second groups. Survival rates were positively correlated with pupal weights, and both variables further discriminated within groups, with larvae fed clones, or switching from aspen to clones, having lower weights and decreased survival rates than larvae fed aspen or switching from clones to aspen. In the southern experiment with maple as the natural host, survival rates discriminated between larvae fed only maple or switching from maple to clones, from larvae fed only clones, or switching from clones to maple. Larvae in the first groups had lower survival rates than larvae in the second groups. Contrary to larvae switching to aspen, whether in the northern or the southern experiments, larvae switching to sugar maple experienced reduced pupal weights, despite this natural host being slightly superior. Larvae on southern clones had highly variable time to pupation compared to sugar maple, and switching from or to clones did not reduce this variability (Fig. 2).

Survival rate from hatching to pupation was high on aspen in both the northern (mean ± CI 95%: 71.9 ± 12.6 %) and the southern (75.2 ± 43.2 %) experiments. On sugar maple, survival was low (26.9 ± 10.9 %). Larvae on hybrid poplar clones in the northern experiment had a lower survival rate (33.6 ± 7.0 %) than larvae on clones of the southern experiment (66.8 ± 10.3 %). The timing of mortality also differed for larvae on northern and southern clones. Larvae on northern clones experienced significantly greater mortality rates before the fourth instar, while larvae on southern clones experienced significantly greater mortality rates after the fourth instar (Fig. 4).

Survival rates for larvae that experienced host switching followed the rates observed for larvae fed the initial host for their entire development in the cases of switching from aspen to clones (73.3 ± 6.0 %) or from clones to aspen (32.5 ± 7.2%) in the northern experiment, or in the case of switching from clones to aspen (91.1 ± 5.7 %) or to sugar maple (70.6 ± 8.1 %) in the southern experiment. These results can be explained by a low or high mortality rate before the fourth instar, followed by a low mortality rate after the fourth instar (Fig. 4). When the mortality was greater after the fourth instar, such as for larvae feeding on southern clones, the overall mortality in the concerned switching treatments was as it would mathematically expected: increased compared to the mortality rate before switching if it was low, as for larvae switching from aspen (69.2 ± 12.3 %), or little affected compared to the mortality rate before switching if it was high, as from switching from sugar maple (44.3 ± 12.2 %). No correlations were observed between mortality rates and pupal sex-ratios in either the northern ($r = -0.07$; $P = 0.6820$) or the southern ($r < 0.01$; $P = 0.9725$) experiments.

### 1.4.2 Larval growth trajectories and threshold size for pupation

Larval weight at each molt increased somewhat exponentially with time since hatching for larvae in the northern experiment, up until reaching the last larval stage or instar (Figure 1.5a). During the last instar, the growth trajectories changed drastically, the larvae gaining weight at a much slower rate. The growth trajectories varied considerably among treatments. At the end of the first instar, weight gains were similar between diets, despite differences in time to reach the second instar (power-law curve-fitting with a $R^2 = 0.01$, *non-significant slope;* Fig. 1.5a). By the time the larvae reached the fourth instar, and thus before any host switching took place, a clear significant and negative power-law curve described the relationship between weight gain and time since hatching ($R^2 = 0.74$, *significant slope*; Fig. 1.5a),

suggesting that the larvae were not able to compensate the negative effect of diet quality on weight gain by increasing time spent feeding. The differences in larval performance between aspen and the hybrid poplar clones, and among clones, became strongly apparent. At the beginning of the last instar, the negative relationship between larval weight and time since hatching for larvae fed aspen or foliage from northern clones remained, although weakened ($R^2$ = 0.33, *significant slope*; Fig. 1.5a), and with a slope value on the low end of values found for the relationships between pupal weight and time to pupation (Fig. 1.2). Including larval performance data from the host switching treatments nullified the relationship between larval weight and time since hatching ($R^2$ = 0.04, *non-significant slope*; Fig. 1.5a), again a result similar to what was observed in the relationship between pupal weight and time to pupation.

In order to achieve greater weights, FTC larvae in the northern experiment increased time spent feeding by increasing the number of instars to reach the pupal stage (Fig. 1.5a). Whereas they completed their larval stage within five instars on aspen, on clone BM2, when switching from aspen to all three northern clones, or from clone BM2 to aspen, the larvae had to spend one more instar on clone BM1 and two more instars on clone MB3 and when switching from clones BM1 or MB3 to aspen. The minimum larval weight that needed to be reached to complete an ultimate instar before pupation is ca. 149 mg. Although larval weight at each instar was not measured for the southern experiment, in only three instances did the larvae completed six instars prior to pupation instead of five (Fig. 1.5b), all instances involving the southern DN3 clone (either alone or when switching to aspen or sugar maple), suggesting that in all other cases the larvae reached a critical weight threshold at the onset of the fifth instar. Taken together, time since hatching, and generally individual instar durations, were more variable in the northern than in the southern experiment. These differences in variability can already be seen in the time window

during which the FTC larvae enter the fourth instar, about twice larger for the northern than for the southern experiment (Fig. 1.5a,b).

The slopes of the growth trajectories, calculated on logged mean replicate weights, can help understand why significant relationships between larval or pupal weight with time to reach a given instar or pupation where obtained for larvae fed foliage solely from natural hosts or clones. As the slope of the growth trajectory increases, the likeliness of overshooting the threshold size for pupation was found to also increase (Fig. 1.6a). This relationship is significant ($F_{1,23} = 11.88$, $P = 0.0022$) with a strong slope for the pooled replicates of the aspen and aspen to clones feeding treatments (for which an ANCOVA analysis could not detect a significant difference). As overshooting the threshold size for pupation increased, pupal weights also increased for both larvae fed aspen or switching from aspen to clones, but with a higher intercept in the former than in the latter treatment (Fig. 1.6c; ANCOVA: $F_{1,22} = 13.93$, $P = 0.0012$). The relationship was not significant for larvae that switched from clones to aspen (Fig. 1.6c; $F_{1,4} = 0.708$, $P = 0.4475$). Between-instar weight ratios (Fig. 1.6b) were not constant during larval development in none of the treatments, indicating that larval growth in FTC is not purely exponential or geometric. Rather, these ratios initially increase and then decrease as the larvae near pupation. There was a strong convergence of ratio values at the beginning of the ultimate instar and at pupation, although small variations at these stages can translate in large differences in absolute weight. This can be seen in the pupal weight differences between the aspen and clones feeding treatments (Fig. 1.2 and Fig. 1.5a). Larvae that switched from clones to aspen benefitted of the higher quality of the natural host diet; however, the switch occurred too close to what appears to be a constant weight ratio for FTC larval development at later stages (Fig. 1.6b).

Pupal sex-ratios were not influenced by larval performance. Sex-ratios in the northern experiment were not correlated with female ($r = -0.03$; $P = 0.8767$) or male ($r < 0.01$;

$P = 0.9973$) pupal weights, neither with development times of females (r = -0.09; $P = 0.6203$) or males (r = -0.06; $P = 0.7236$). Sex-ratios in the southern experiment were also not correlated with female (r = -0.07; $P = 0.6548$) or male (r = 0.17; $P = 2424$) pupal weights, neither with development times of females (r = -0.06; $P = 0.6920$) or males (r = -0.13; $P = 0.3832$).

### 1.4.3 Water and nitrogen contents in relation to larval performance

Results from multiple regression models indicate that the water and nitrogen contents of the hosts foliage were most often significant variables related to FTC pupal weight and time to pupation. Fifty percent of the models have coefficients of determination ($R^2$) greater than 0.73 (Table 1). However, based on the partial $R^2$ values, the nitrogen content contributed the most or equally with the water content to the models $R^2$ in a majority of models, and always with estimate signs in agreement with expectations. When the estimate signs for the water content were opposite to expectations, it was also the case that this variable generally contributed less to the models $R^2$. In only two cases, the water content contributed the most to the models $R^2$ with estimate signs opposite to expectations. When both the nitrogen and water contents contributed equally and additively to the models $R^2$, the estimate signs were in agreement with expectations. To summarize, in a majority of models, the nitrogen content explained the most, or equally with the water content, the observed variations in pupal weight (increasing effect) and in development time (decreasing effect), and in most cases for this majority of models, it was the averaged weighted mean foliage content before the fourth instar that was retained during model selection. However, if the variations in development time were systematically well and coherently explained by the models, whether or not they included data from the hosts switching experiments, it proved more difficult for variations in pupal weight, which is

understandable since it has been shown in the present study that weight gain adjustment is more complex for FTC larvae. Variations in time to pupation for larvae in the northern experiment were mainly explained (models $R^2$: 0.76-0.96) by the averaged weighted mean nitrogen content before the fourth instar. Variations in time to pupation for larvae in the southern experiment were mainly explained (models $R^2$: 0.64-0.92) by the averaged weighted mean nitrogen and water contents before the fourth instar. Models for pupal weights in the northern experiment were inconsistent between sexes and when data from the hosts switching experiments were included. Models for pupal weights in the southern experiment were consistent between sexes, but inconsistent when data from the hosts switching experiments were included.

### 1.4.4 Hosts and insect phenologies

All clones, whether northern or southern, except northern clone BM2, broke buds later (by six to ten days, depending on the comparison) than their natural hosts, in Ripon, Quebec (Fig. 1.7). There was a difference of the same magnitude between the budbreak Julian days (JD) for aspen between the years of the northern (JD: 126) and the southern (JD: 134) experiments. The months of February through April of the year of the northern experiment were exceptionally warm, with temperatures close or above the 1971-2000 daily maxima, while spring temperatures in the year of the southern experiment were close to the climatic normals (Environment Canada, 2013). Differences in budbreak dates were nonetheless expected given the differences in hardiness among clones (Fig. 1.1), and justified the use of foliage of similar phenology from aspen and from clones to minimize host phenology effects on FTC larvae. This approach thus allows the comparison of insect phenologies. Host switching from southern clones to sugar maple (determinate growth) may have exposed FTC larvae to foliage of lesser quality because of differences in phenology

that are exacerbated in Ripon compared to more southern locations, but sugar maple is already a poorer host.

Examination of insect phenologies, and especially the time frame for adult emergence, is important from a resistance development perspective, given the short life span of FTC moths, and their concomitant readiness to mate as they emerge. From the literature (Hodson, 1941), a difference of ten days in peak emergence from different hosts is likely to be sufficient to greatly reduce mating opportunities. To make sure that our development time results can be interpreted directly, pupation to emergence times were tested among feeding treatments from all experiments. Pupation to emergence times among feeding treatments were not significantly different in the northern experiment, females took 17.4 ± 0.6 days to emerge (ANOVA; $F_{9,22} = 1.10$, $P = 0.40$) and males took 18.2 ± 0.6 (ANOVA; $F_{9,25} = 0.75$, $P = 0.66$). In the southern experiment, no differences were found for females who took 17.8 ± 0.6 days to emerge (ANOVA; $F_{15,31} = 1.07$, $P = 0.41$), but differences were found for males, who took in mean 18.5 ± 0.5 days to emerge (ANOVA; $F_{15,30} = 3.52$, $P = <0.01$), although treatments differed of only one day.

Mating between moths from aspen and from northern clones is not likely (Fig. 1.7), even taking into account that hosts phenologies may be more similar in plantations located in northern Quebec. Fifty percent of the larvae fed aspen pupated in 30-31 days after hatching while it took clone-fed larvae from 42 to 57-59 days, depending on the clone (Fig. 1.7). Larvae that switched from aspen to the northern clones had median pupation time intermediate (36-39 days) between aspen- and clone-fed larvae, and the emerging moths would contribute to dilute mating among moths that would develop solely from clone BM2 (42 days), but very little among moths that developed from clones BM1 (49-50 days) and MB3 (57-59 days). A similar pattern of segregation in time was observable for larvae fed aspen (30-33 days) and clones (34-49 days) in the southern experiment, especially with larvae fed clone DN3 (46-49

days). Similarly, larvae that switched from aspen to the southern clones had intermediate median pupation time (33-37 days). Additionally, moths that would emerge from sugar maple (47-51 days), and from larvae that switched from sugar maple to the southern clones (40-48 days), would be synchronized to mate with moths that would develop from the southern clones. Interestingly, moths that develop from aspen and from maples appear to be segregated in time.

## 1.5 Discussion

Results show that the recommended hybrid poplar clones for the northern regions of Quebec selected for the present study are relatively resistant compared to the larval performance observed on quaking aspen, the dominant natural host of this species in these regions. Indeed, all performance variables (survivorship, time to pupation and pupal weight) were negatively affected when FTC larvae were fed foliage from these clones. In contrast, the performance of FTC larvae on clones recommended for the southern regions of Quebec was somewhat intermediate between its two main natural hosts, sugar maple and quaking aspen. In both the northern and southern experiments, larvae that switched from aspen to clones reached lower pupal weights than when fed only aspen, but they took less time to reach pupation and experienced less mortality than those larvae that fed only on clones. This suggests that clone resistance would be greatly reduced when larvae migrate from aspen stands to plantations. These results were expected and are in agreement with observations that inadequate, or less adequate, diets for young larvae become acceptable to older larvae in polyphagous Lepidoptera (Hwang et al., 2007; Robison and Raffa, 1997, 1994) and that the host consumed by young larvae has a large influence on overall larval perfomance (Stoyenoff et al., 1994).

The performance of FTC larvae on southern clones was little affected compared to that on sugar maple. Survivorship was even better on clones than on sugar maple. Although switching from an *Acer* host to *Populus* hosts would be considered demanding, the performance of FTC larvae in such a situation appears to be seldom affected, or even to be slightly improved. Compared to aspen, the performance of FTC larvae on both sugar maple and southern clones was decreased.

### 1.5.1 Emerging growth model for the forest tent caterpillar

On all the diets FTC larvae experienced in this study, time to pupation was the single variable to be systematically and negatively affected compared to the best host, quaking aspen. Time to pupation was much variable among northern clones (37 days) and southern clones (17 days). Robison and Raffa (1994) reported – in one of the rare other study of FTC performance on hybrid poplar clones - that time to pupation varied by 18 days on 14 clones. Comparatively, Hemming and Lindroth (1995) observed a variation of only 4 days in time to pupation for FTC larvae fed on 7 quaking aspen clones, despite there was a 60% difference between the largest and smallest mean pupal weights registered on those clones. A similar difference of 4 days on aspen was observed by Lorenzetti et al. (1999) and by Trudeau et al. (2010), also despite a large difference in pupal weights, as reported in Fig. 1.2 of this paper. On the other hand, these authors reported differences in time to pupation of 14 days for males and of 18 days for females for FTC larvae fed sugar maple for very small variations in pupal weights (Fig. 1.2). The pattern that emerges from this and other studies is that short development times are generally associated with large variation in pupal weights and that long development times are generally associated with small variations in pupal weights.

The large variation in development time observed in this study is matched by a variation in the number of larval instars (5 to 7; Fig. 1.5a,b). The number of instars is often considered to be fixed for a given species, but a review by Esperk et al. (2007) indicates that on the contrary, variations are quite often observed. Plasticity in the number of instars may have evolved as a means to cope with an unfavorable environment. Although a prolonged development time is often cited as detrimental to insect herbivores because it correlates with increased predation risks and with a seasonal decrease in diet quality (Parry et al., 1998), it may be concluded that other selection pressures led to a more plastic strategy in larval development. The FTC being an early spring feeder (Stehr and Cook, 1968), it may be that in the northern portion of its distribution, which include northern USA and Canada, cold spring spells that limit feeding activity are a sufficiently recurrent feature of this insect environment that it exerted a stronger selection pressure (because it is experienced by all individuals simultaneously) than that exerted by natural enemies. Thermoregulation (by group basking) is a readily occurring behavior in this species (McClure et al., 2011) and in other *Malacosoma* spp. (Fitgerald, 1995).

A low quality diet has previously shown to increase development time and the number of instars in FTC larvae (Jones and Despland, 2006). It has also been shown that an increase in the number of instars is not only a corollary of increased development time, but a means to reach a critical threshold weight beyond which pupation can take place (Etilé and Despland, 2008). A critical threshold weight for pupation was first evidenced by Nijhout (1975) in the tobacco hornworm, *Manducta sexta* (L.). The threshold weight to pupate in the present study for both sexes combined was estimated to be 149 mg, which is very close to the critical weight of 140.5 reported by Etilé and Despland (2008) for female FTC larvae.

The existence of a threshold size for pupation, reached through variation in development time, does not necessarily translate into reduced variation in final size.

As shown in Fig. 1.2 for FTC larvae fed on natural hosts and clones, there is a strong negative relationship between pupal weight and time to pupation. Observations by Robison and Raffa (1994) for FTC larvae on hybrid poplars support this negative relationship. With the objective of conciliating the presence of a threshold size for pupation and the observed variation in final size, we hypothesised that the slope of larval growth trajectories (i.e., their growth rates, e.g. Fig. 1.5a) influences the achievable final size. Given that insect development is constrained by molts, this hypothesis predicts that the greater the slope of the larval growth trajectory, the greater the likeliness of overshooting the threshold size to pupate. Theoretically, this prediction is demonstrable. Empirically (Fig. 1.6a), we have shown that there is a positive relationship with a strong slope ($\beta$ = 792.1) between growth trajectories, calculated as the observed growth rates during the 4th through the penultimate instar, and the difference between the size at the onset of the ultimate instar and the threshold size to pupate. It has further been shown that this latter difference can be used to predict pupal weights in most cases (Fig. 1.6c). Although Robison and Raffa (1994) did not explicitly show it, it is possible to see this positive relationship between pupal weights and growth rates in their data for FTC. Our hypothesis could also explain the large variation in pupal weight for small variations in development time when FTC feeds on aspen, and conversely the small variation in pupal weight for large variations in development time when FTC feeds on sugar maple (Fig. 1.2).

Despite the strong slope found for our empirical model (Fig. 1.6a), there is quite a large variability between the size at the onset of the ultimate instar and growth trajectories. This variability is particularly associated with larvae that were switched from aspen to clones and from clones to aspen. Larvae in these treatments did not either conform the negative relationship between larval (Fig. 1.5a) or pupal (Fig. 1.2) weights and development time. Ontogenic variations in empirical between-instar weight ratios (Fig. 1.6b) suggest a complex adjustment of weight gain during larval development in FTC larvae. In none of the treatments did FTC larvae expressed a

purely exponential or geometric growth trajectory, which would translate into a constant between-instar weight ratio. Rather, these ratios initially increase and then decrease as the larvae near pupation. Interestingly, larvae in the different treatments converged to similar ratios at the beginning of the ultimate instar and at pupation. This convergence may explain why our model does not hold for larvae switching from clones to aspen: the benefit of switching to a better diet occurs too close to the final, somewhat diet-independent, growth ratios.

### 1.5.2 Switching hosts: instar-dependent or size-dependent?

In this study, we have chosen to operate diet switching at the onset of the fourth instar to facilitate comparison among treatments, but also because there is a pervasive perception from the literature that FTC larvae become less sedentary once they have reached that particular stage. However, in reality, increased mobility may be more size-dependent that instar-dependant. Despland and Hamzeh (2004) have shown that FTC larvae become more solitary as a result of an ontogenic shift in behavior when a certain size has been reached. In the context of the present study, however, the practical implication is that host switching would occur later than it was implemented, in particular for larvae on clones and on sugar maple. In the latter case, and in general, it should be kept in mind that if larval migration should rather take place during the last instar, its duration is quite similar among diets (Fig. 1.5) and represents 40% or more of the total larval development time. It is also at this stage that they double their size (Fig. 1.6b) from an already large weight, meaning that they will consume a large amount of food during that last stage.

### 1.5.3 Phenology of FTC development and deployment of plantations

Considering that FTC, as a capital-breeder, does not feed at the moth stage and consequently, the adult life span is short – five days or less according to Hodson (1941), the window of opportunity for reproduction is quite small. An increase in FTC development time, as it will occur when feeding on relatively more resistant hosts will also mean an increase in reproductive isolation from individuals that feed on more adequate hosts, which could lead to the rapid emergence of counter-resistance (Robison, 2002). This may occur on clones recommended for the northern regions of Quebec unless proper plantation deployment measures are implemented (see Fig. 1.7). Locating hybrid poplar plantations in northern Quebec near aspen stands may help dilute resistance genes by facilitating migration by larvae, which in turn will take more time to become moths, but it will be at the expense of increased defoliation, even likely in between outbreaks. Locating plantations close to non-host stands would decrease the risk of defoliation, but the size of those plantations may need to be small to avoid the presence of endemic FTC populations. However, plantations embedded in a mixed host/non-host landscape matrix may benefit from reduced outbreak duration (Charbonneau et al., 2012). Or, hybrid poplar plantations may be envisioned to be directly mixed with non-host trees to increase the impact of natural enemies (Jactel and Brockerhoff, 2007). It is interesting to note that given the variation in development time observed on the different northern clones in this study, a mixture of clones in a single plantation would not provide, as often stated (Gould, 1991; Hurley et al., 1997; Hühn, 1986), a fail-safe for the development of counter-resistance, at least in FTC. In the southern regions of Quebec, FTC may more readily interbreed if feeding on the different recommended clones (Fig. 1.7). Moreover, FTC in plantations may interbreed with FTC that migrated from sugar maple stands, either as larvae or as moths. Given that the recurrence of FTC outbreaks is less in maple-dominated regions than in aspen-dominated regions (13 vs 9 years; Cooke and Lorenzetti, 2006), and that FTC larvae feed on most hardwood species – thus making

it difficult to 'hide' plantations in a non-host matrix, there may be no better economically feasible alternatives than to have plantations next to sugar maple stands.

### 1.5.4 Resistance factors in light of the FTC response to an inadequate diet

Hybrid poplar secondary chemistry was not investigated in the present study. Regression analyses based on water and nitrogen contents of natural hosts and hybrid poplar clones foliage fed to FTC larvae during their first four instars yielded models that explained between 86 and 96 % of the variation in mean time to pupation (Table 1). These results do not necessarily imply that the secondary chemistry of hybrid poplars is irrelevant since primary and secondary chemistries can be auto-correlated (Mattson and Scriber, 1987).

In light of the FTC response to an inadequate diet, that is prolonged development time, which implies longer feeding periods and possibly the risk of adapted biotypes, other avenues must be evaluated to increase our capacity to manage hybrid poplars on the long term. One avenue of research that could be intensified as a first line of defense of hybrid poplar plantations is resistance against oviposition by FTC moths. Oviposition resistance could in theory reduce the number of years isolated plantations would be under FTC attack. Though, this avenue would likely involve large screening trials. In their study, Robison and Raffa (1994) found no differences in FTC oviposition among hybrid poplar clones. In another study with the cottonwood leaf beetle (*Chrysomela scripta* F.), oviposition preference was found in multiple-choice tests, but not in no-choice tests (Bingaman and Hart, 1992a). In the case of the poplar and willow borer (*Cryptorhynchus lapathi* L.), hybrids with a *P. maximowiczii* parentage were less preferred (Broberg and Borden, 2005). Inducible defenses could be another avenue as tree resources are only mobilized when under attack, and during

low density FTC populations only a fraction of the trees would be induced. However, no correlation has been found between constitutive and inducible levels of defense in hybrid poplars, not all clones are inducible, and inducibility depends on leaf age (Robison and Raffa, 1997). Constabel et al. (2000) found a negative effect on FTC feeding of induced polyphenol oxydase in a hybrid poplar, but this effect decreased with leaf age. This resistance mechanism is interesting because it may decrease damage by FTC larvae at low to intermediate population levels, but may not prevent damage by migrating larvae from natural aspen stands. Though, a transgenic poplar overexpressing inducible polyphenol oxydase was found to be more effective against weaker FTC larvae (Wang and Constabel, 2004). Induced emission of terpenes may be a more complex avenue because tri-trophic interactions are involved (Arimura et al., 2004; Mondor and Roland, 1998), but may prove more long-lasting, and compatible with the general FTC response to an inadequate diet.

A combination of approaches could be considered, for example intrinsic resistance and the application of the insecticide *Bacillus thuringiensis* (Bt). The application of a biological insecticide might nevertheless need to be part of a protection strategy since plantations would be at risk when FTC population are at very high density during an outbreak. Research in this area is needed, especially in the light that the efficacy of Bt on the Gypsy moth (*Lymantria dispar* L.) varies depending on the clone, and independently of resistance (Broderick et al., 2010). To our knowledge, there has not been any study on the interaction between Bt and hybrid poplar resistance with the FTC. However, Kouassi et al.(2001) reported a 100-fold difference of efficacy of Bt on FTC larvae when fed sugar maple than when fed aspen. One challenge with the use of Bt applications in the context of hybrid poplar plantations would be the proper timing of spraying because of the elongated period of time when larvae of different sizes are present (Fig. 1.7).

## 1.6 Conclusion

Our finding that FTC larvae respond to variations in the relative resistance of hybrid poplar clones by mainly increasing their time to pupation, with the consequence that the non-feeding moths may be reproductively isolated depending on the clone, should stimulate reflection by managers who design the deployment of hybrid poplar plantations. Unlike FTC, other potentially important hybrid poplar insects, like the large aspen tortrix *Choristoneura conflictana* (Walker), the gypsy moth *Lymantria dispar* (L.) (Humble and Stewart, 1994) and the cottonwood leaf beetle *Chrysomela scripta* (F.) (Bingaman and Hart, 1992b), are not capital breeders and adults live longer than FTC moths, so their window of opportunity are large enough to minimize reproductive isolation if clonal resistance also leads in these species to differences in development time. Polyclonal plantations are promoted in the technical literature, sometimes with little more than a mention that it is a strategy to minimize risks, and rarely with guidance on how to select clones depending on the risk, when in fact, there are two underlying different management approaches. First, mixtures of clones are intended to decrease risks at large, biotic or abiotic, by minimizing the likelihood of all clones being simultaneously affected. This strategy requires the deployment of many different clones in the same plantations with the objective of minimizing losses and maximizing productivity (Coyle et al., 2002; Hühn, 1986). The second management approach addresses directly the issue of the development of resistant insect biotypes by maximizing the opportunity of reproduction between resistant and non-resistant insects (Gould, 1991; Hurley et al., 1997; Raffa, 1989). This is accomplished by deploying susceptible and resistant clones in the same plantations. Both these strategies could work to minimize the impacts of FTC on plantations and the opportunity for resistant biotypes, if they are implemented taking into account the plasticity in development time that has been demonstrated for this insect. Because risks to plantations are numerous, a polyclonal plantation with many clones could address simultaneously others risks and the FTC particularity by making sure that

emergence from the different clones are overlapping sequentially, providing some level of dilution of counter-resistance genes. This approach would essentially mimic the natural clonal diversity found in aspen stands (Lindroth and St. Clair, 2013). Alternatively, the deployment of a few equally resistant clones, but expressing different mechanisms of resistance selecting for unrelated counter-resistance genes, could be a good strategy to maintain a dilution effect among emerging moths (Coyle et al., 2002; Roberds and Bishir, 1997; Robison, 2002). The FTC is a special case and it is important to treat it specifically considering its significant pest status in North America. The information provided here is timely in the perspective of developing new hybrid poplar clones.

## 1.7 Acknowledgements

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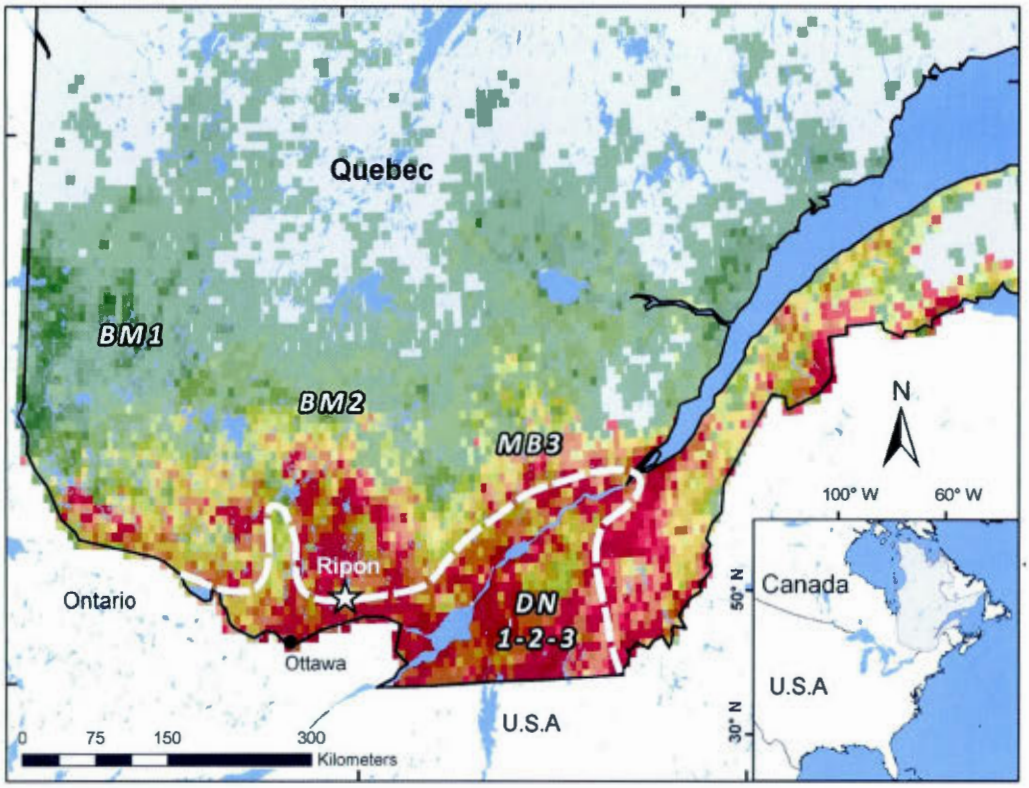
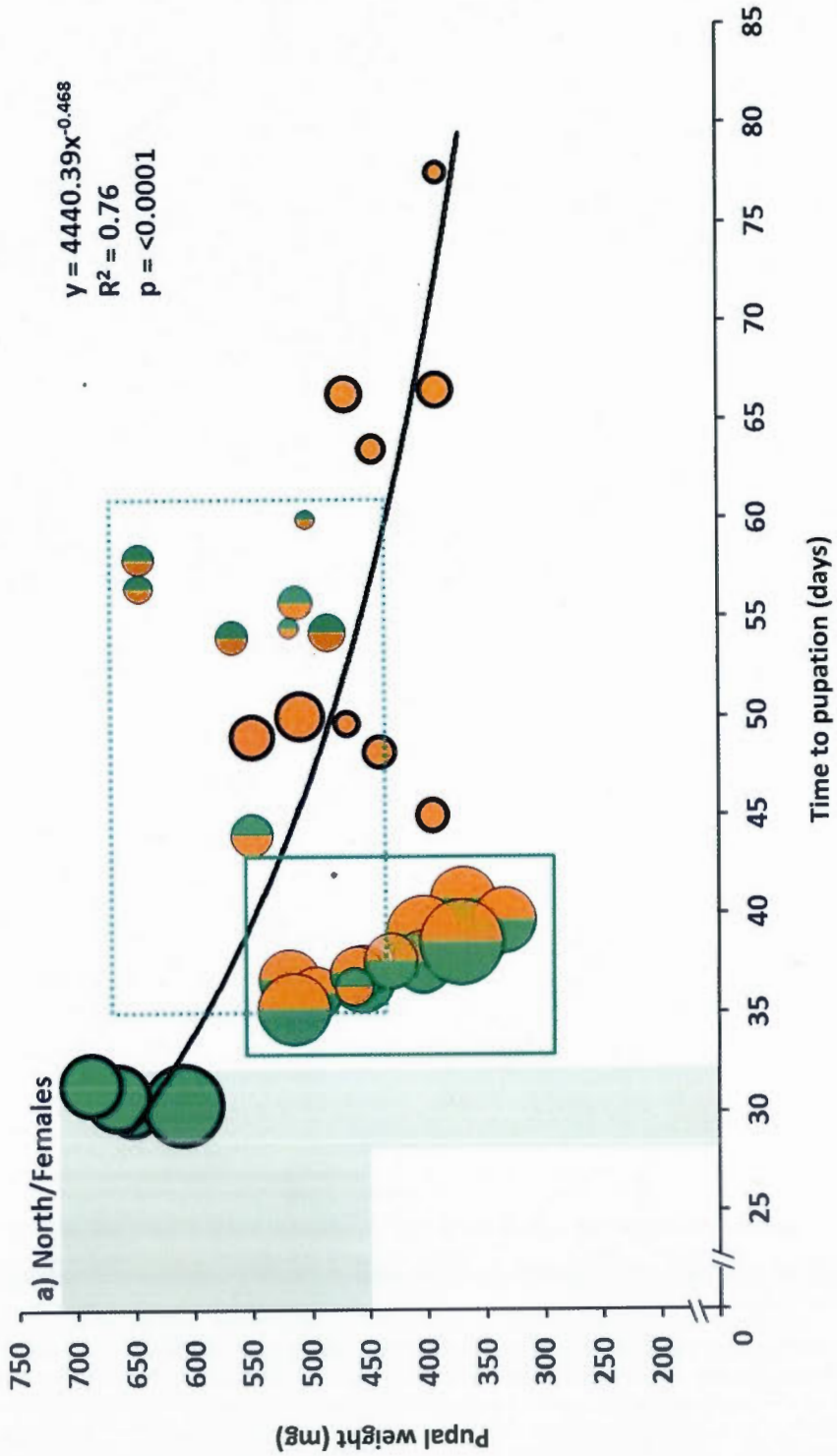
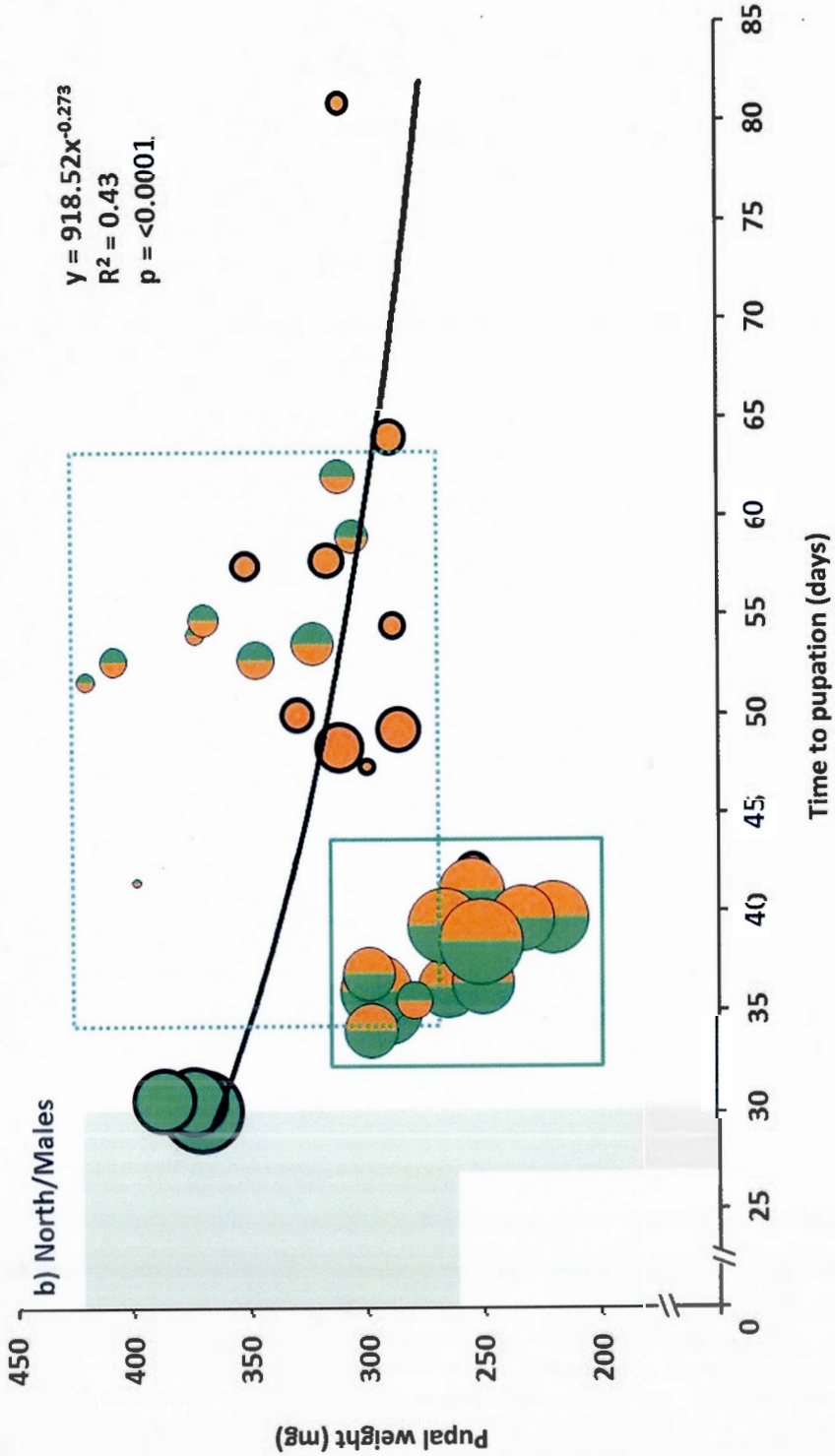
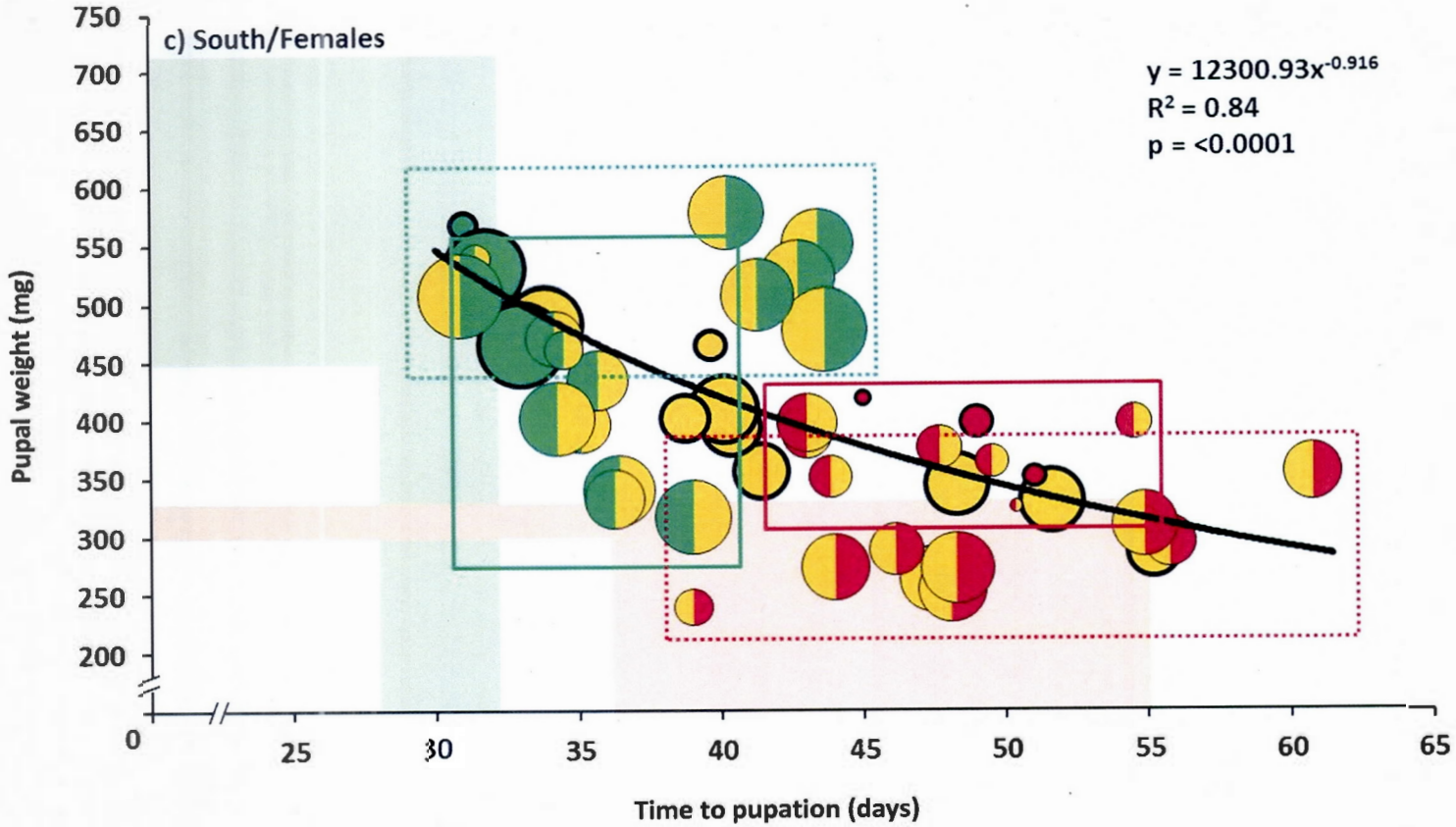



**Fig. 1.1.** Map showing regions of Quebec for which plantations of the hybrid poplar clones used in this study are recommended by the Quebec Ministry of Natural Resources. The limit between the northern and the southern zones, depicted by a thick white dashed line, is based on the delineation between major bioclimatic domains (Saucier et al., 2011 ). Northern clones (BM1, BM2 and MB3) are all hybridizations between *P. balsamifera* and *P. maximowiczii*. Southern clones (DN1, DN2 and DN3) are all hybridizations between *P. deltoides* and *P. nigra*. The underlying shades of green and red represent the various proportions ofbasal areas of quaking aspen (*Populus tremuloides* Michx.) and sugar maple (*Acer saccharum* Marsh), respectively. The darker the color, the greater the absolute combined basal areas of the two natural hosts of the FTC (*Malacosoma disstria* Hbn.). Yellows indicate equal contribution of quaking aspen and sugar maple to the absolute basal area. The location of the common hybrid poplar clones plantation in Ripon is indicated by a white star.


a) North/Females
y = 4440.39x^-0.468
R² = 0.76
p = <0.0001
Pupal weight (mg)
Time to pupation (days)
750
700
650
600
550
500
450
400
350
300
250
200
0
25
30
35
40
45
50
55
60
65
70
75
80
85


b) North/Males
y = 918.52x^-0.273
R² = 0.43
p = <0.0001
Pupal weight (mg)
Time to pupation (days)
450
400
350
300
250
200
0
25
30
35
40
45
50
55
60
65
70
75
80
85


c) South/Females
y = 12300.93x^-0.916
R² = 0.84
p = <0.0001
Pupal weight (mg)
750
700
650
600
550
500
450
400
350
300
250
200
0
25
30
35
40
45
50
55
60
65
Time to pupation (days)

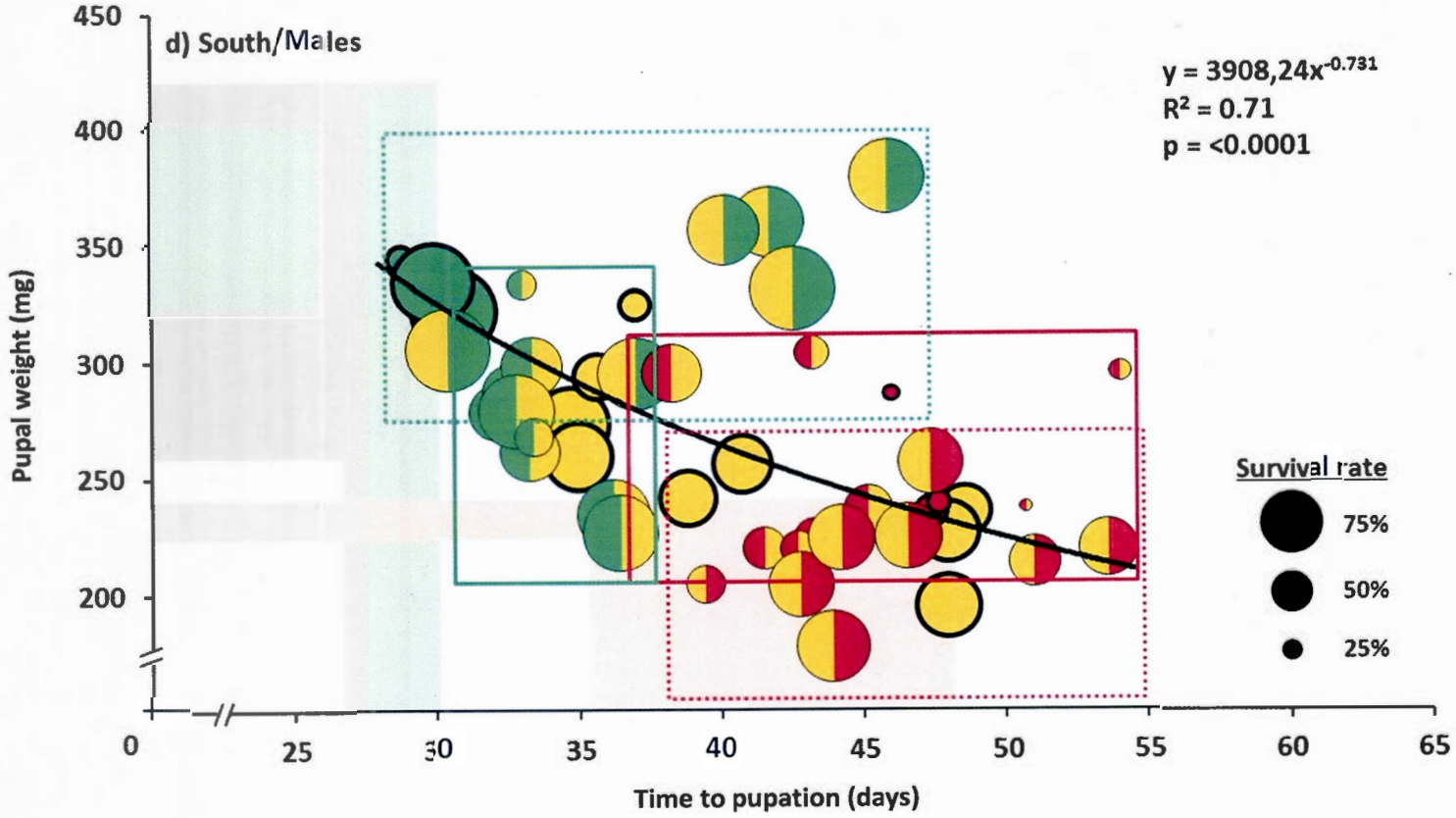

d) South/Males
y = 3908,24x^-0.731
R² = 0.71
p = <0.0001
Survival rate
75%
50%
25%
Pupal weight (mg)
Time to pupation (days)
450
400
350
300
250
200
0
25
30
35
40
45
50
55
60
65

**Fig. 1.2.** Pupal weight in relation to time to pupation for FTC larvae fed foliage of natural hosts (quacking aspen or sugar maple), hybrid poplar clones from a common plantation in Ripon, Quebec, or switching at the fourth instar from natural hosts to clones, or from clones to natural hosts. a) and b) : results from the northern experiment in which hybrid poplar clones recommended for the north of Quebec were tested. c) and d): results from the southern experiment in which hybrid poplar clones recommended for the south of Quebec were tested. Results of both experiments are presented separately for females (a) and c)) and for males (b) and d)). Replicate values are presented for each treatment. Bubble size indicates survival rate; the corresponding legend appears at the bottom right of graph d). Bubbles with thick outlines are replicate values for larvae fed foliage of natural hosts (aspen, shown in green and sugar maple, shown in redor of hybrid poplar clones (Northern experiment clones: dark orange. Southern experiment clones: light orange.). Bubbles with thin outlines and with two colours are replicate values for larvae switching at the fourth instar from natural hosts to clones, or from clones to natural hosts. The colors on the left and right sides of the bubbles identify the host before or after switching, respectively. Power curves (thick black lines) for the relationships between pupal weights and time to pupation for larvae fed foliage of natural hosts or clones are presented, along with estimated equations, R-squared values and p values. Solid and dotted line boxes: spread in the X-Y plane of replicate values for larvae switching at the fourth instar from natural hosts to clones, or from clones to natural hosts (aspen to, or from, clones: green; sugar maple to, or from, clones: red), respectively. Colored zones represent size and time at pupation ranges on aspen (light green) and sugar maple (light tan) observed in other studies (Lorenzetti et al. 1999; Trudeau et al., 2010) (see text for details).

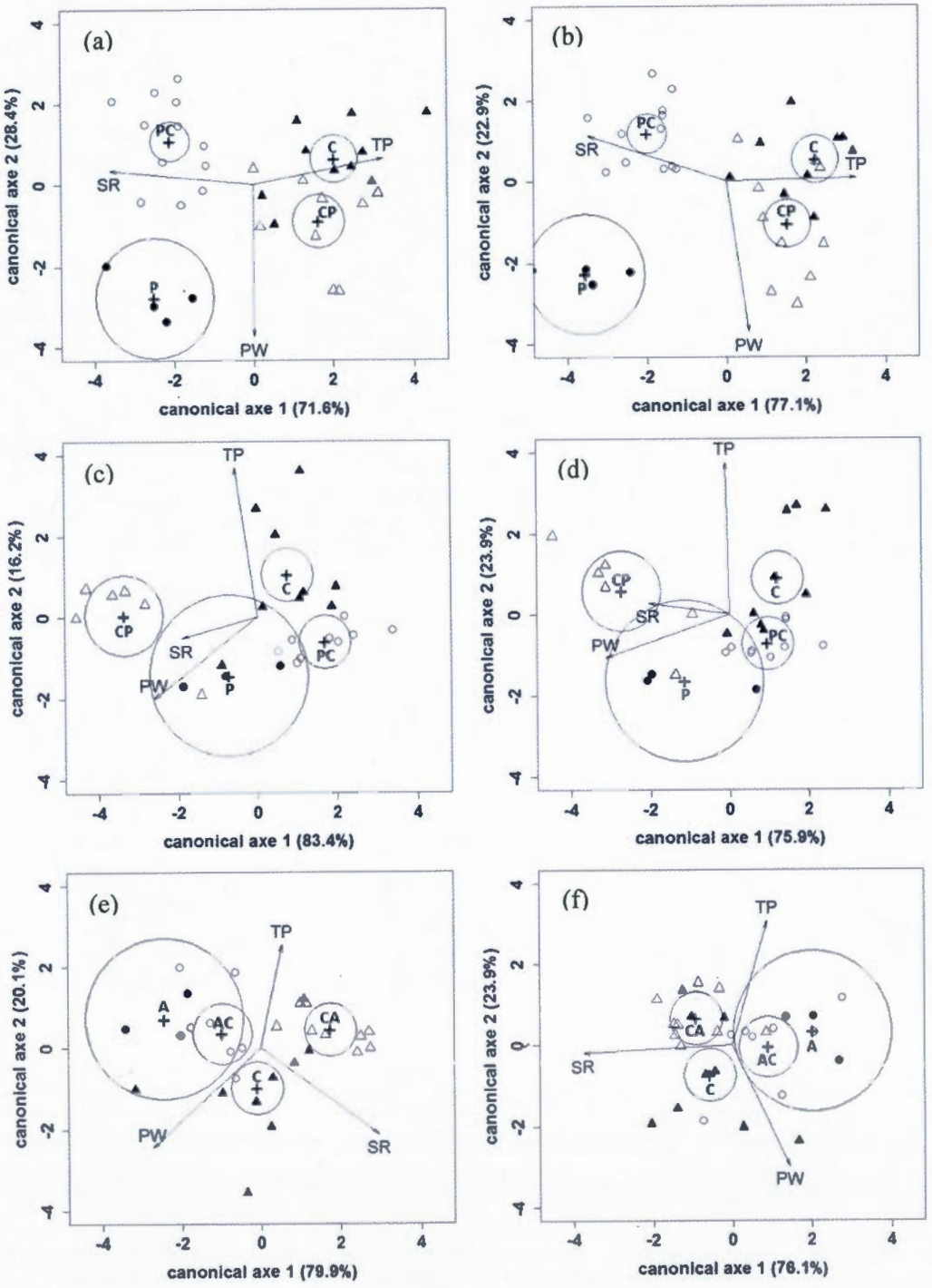

(a)
canonical axe 2 (28.4%)
canonical axe 1 (71.6%)
PC
C
TP
SR
CP
P
PW
(b)
canonical axe 2 (22.9%)
canonical axe 1 (77.1%)
PC
SR
C
TP
CP
P
PW
(c)
canonical axe 2 (16.2%)
canonical axe 1 (83.4%)
TP
C
CP
SR
PC
PW
P
(d)
canonical axe 2 (23.9%)
canonical axe 1 (75.9%)
TP
CP
C
SR
PC
PW
P
(e)
canonical axe 2 (20.1%)
canonical axe 1 (79.9%)
TP
A
AC
CA
C
PW
SR
(f)
canonical axe 2 (23.9%)
canonical axe 1 (76.1%)
TP
CA
SR
AC
A
C
PW

**Fig.1.3.** Results of canonical discriminant analyses, with time to pupation (TP), pupal weight (PW) and survival rate (SR) of FTC larvae as independent variables, for the northern experiment (a: females; b: males) and the southern experiment, with aspen (c: females; d: males) or sugar maple (e: females; f: males) as the natural host. Feeding treatments were (P) aspen or (A) sugar maple (filled black circles), (C) clones (filled black triangle), switching from (PC) aspen or from (AC) sugar maple to clones (empty circles), switching from clones to (CP) aspen or to (CA) sugar maple (empty triangles). Treatment means are indicated by a plus sign (+). 95 % confidence regions of the means are indicated by circles.

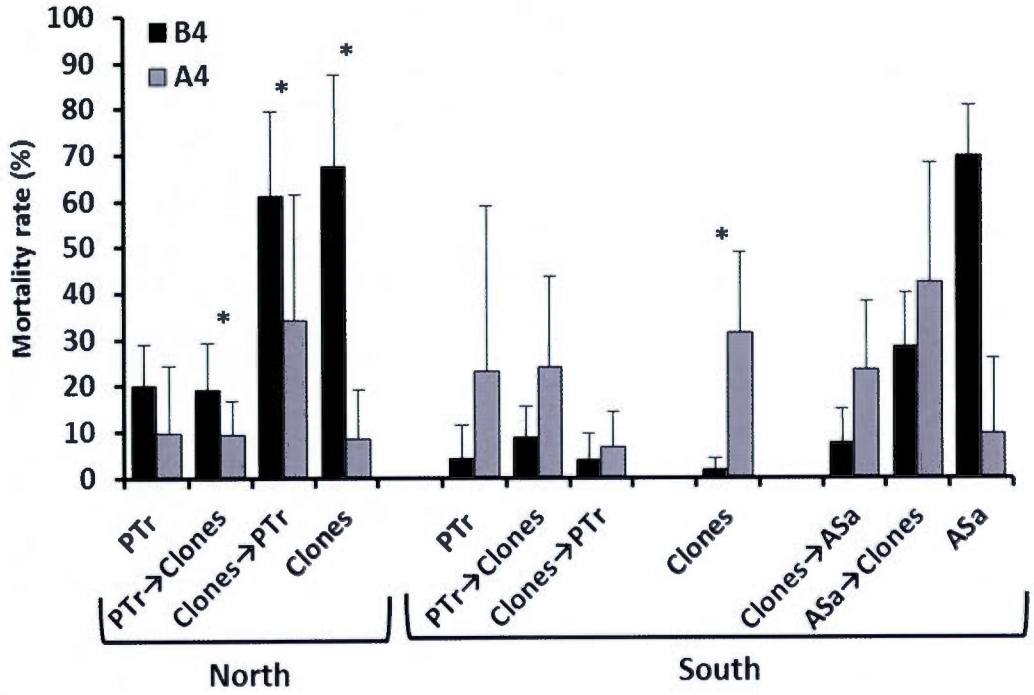
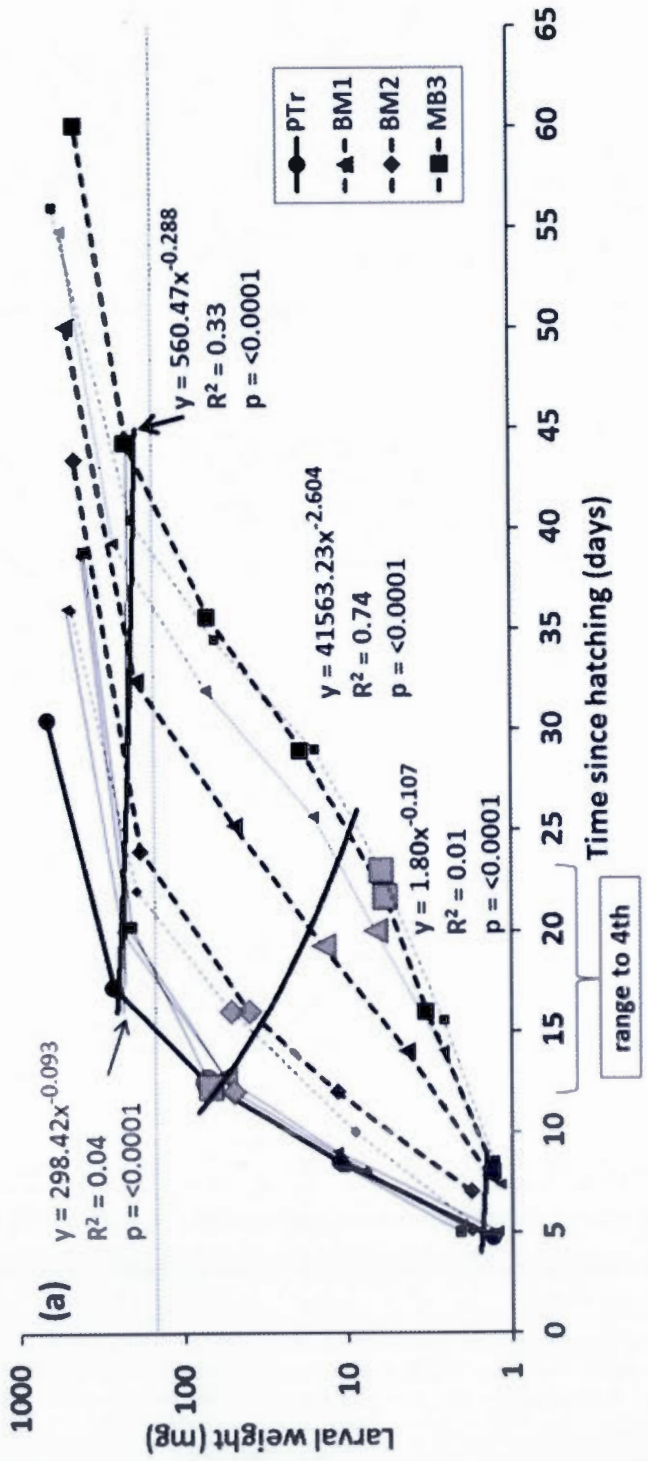



**Fig. 1.4.** Mean (±SD) mortality rates before (B4) and after (A4) the fourth instar for FTC larvae in the northern and southern experiments. Data for the three clones in each experiment were grouped. PTr: quaking aspen (*Populus tremuloides*). ASa: sugar maple (*Acer saccharum*). Asterixes above the bars indicate significant differences between B4 and A4 as determined by Wilcoxon signed-rank (pairwise) tests.


(a)
y = 298.42x^-0.093
R² = 0.04
p = <0.0001
y = 560.47x^-0.288
R² = 0.33
p = <0.0001
y = 41563.23x^-2.604
R² = 0.74
p = <0.0001
y = 1.80x^-0.107
R² = 0.01
p = <0.0001
PTr
BM1
BM2
MB3
range to 4th
Larval weight (mg)
Time since hatching (days)
1000
100
10
1
0
5
10
15
20
25
30
35
40
45
50
55
60
65

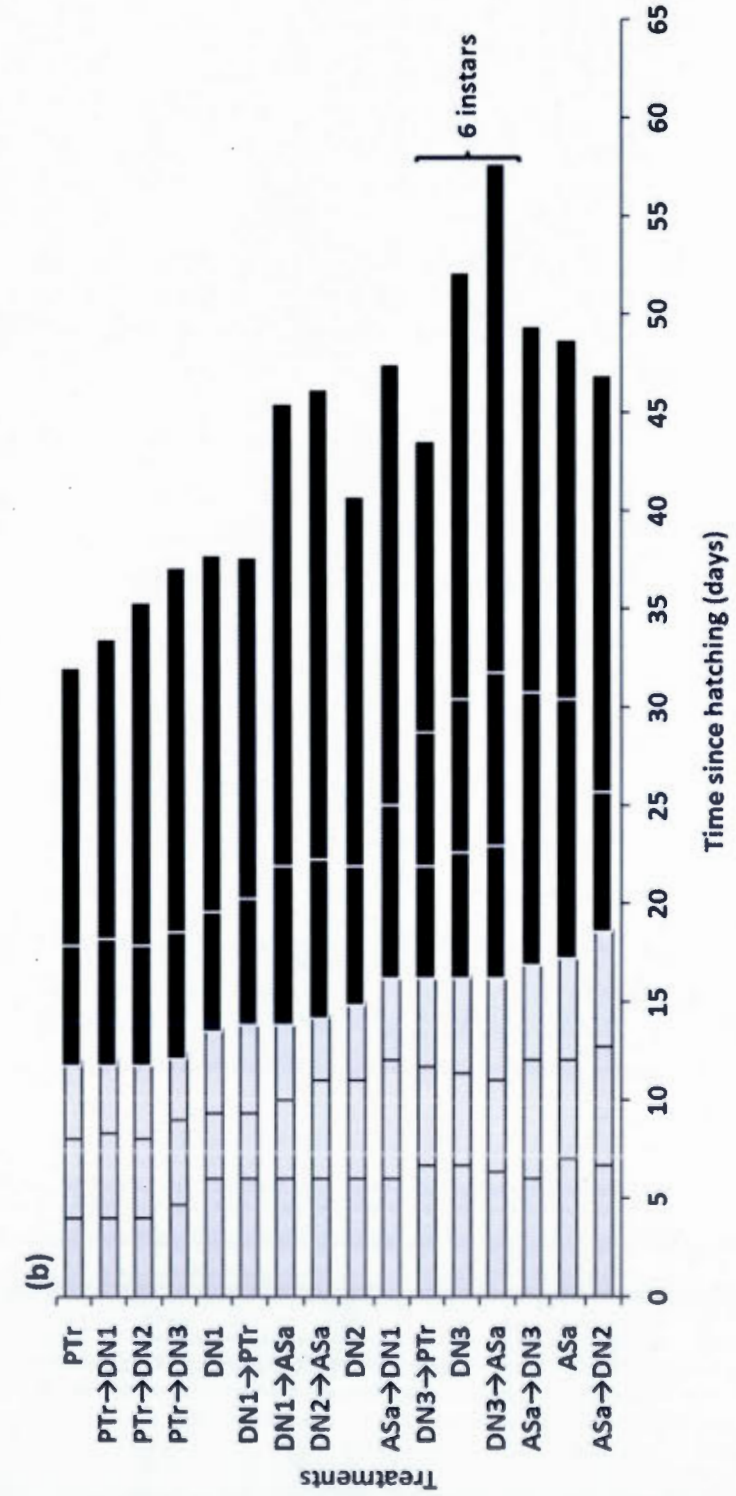

(b)
Treatments
PTr
PTr→DN1
PTr→DN2
PTr→DN3
DN1
DN1→PTr
DN1→ASa
DN2→ASa
DN2
ASa→DN1
DN3→PTr
DN3
DN3→ASa
ASa→DN3
ASa
ASa→DN2
0
5
10
15
20
25
30
35
40
45
50
55
60
65
6 instars
Time since hatching (days)

**Fig. 1.5.** (a) FTC mean larval weight (shown on a log scale) relationships with mean time to reach a given larval stage (instar) or pupation, i.e., growth trajectories, for the northern experiment. Each symbol represents the start of an instar, except for the symbols at the end of the growth trajectories, which are mean pupal weights. Bold growth trajectories: larvae fed foliage from quacking aspen (Ptr; solid line) or from northern hybrid poplar clones (BM1, BM2 and MB3; dashed lines). Thin growth trajectories: larvae switching from aspen to clones (solid line) or from clones to aspen (dashed lines). Power curves for the relationships between larval weights and time since hatching for larvae fed foliage of natural hosts or clones at the start of the $2^{nd}$, $4^{th}$ and the ultimate instars (bold lines) were estimated on replicate treatment values and are presented along with equations and p- and R-squared values. The thin power curve for the ultimate instar includes data for larvae switching at the $4^{th}$ instar from aspen to clones, or from clones to aspen. The dotted line represents the threshold size for pupation. (b) Time since hatching for larvae in the southern experiment: time to complete each of the first three instars (light grey); time to complete the $4^{th}$, $5^{th}$, and $6^{th}$ instars (black; note that only the larvae fed clone DN3, or switching from clone DN3 to natural hosts, completed an extra instar). ASa: sugar maple. DN1, DN2, and DN3: southern hybrid poplar clones. Only female pupal weight and time to pupation were presented.

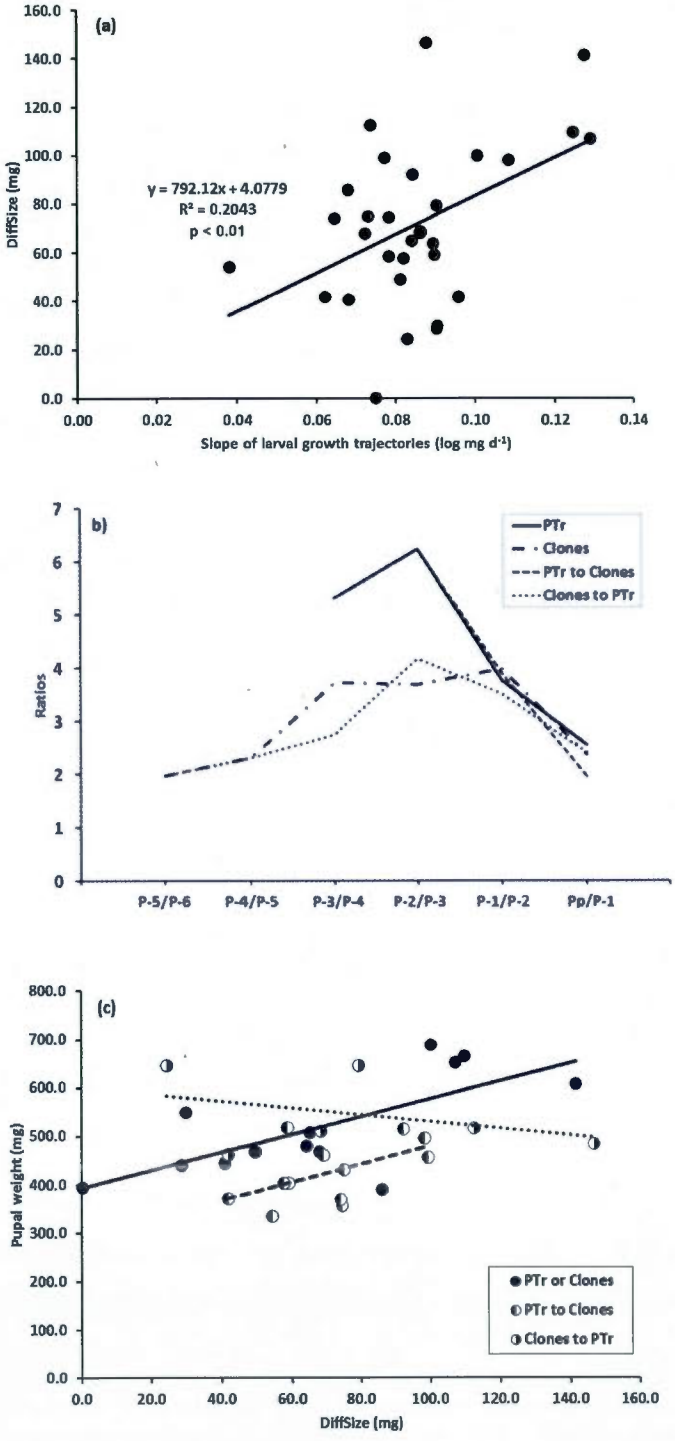

(a)
y = 792.12x + 4.0779
R² = 0.2043
p < 0.01
DiffSize (mg)
Slope of larval growth trajectories (log mg d⁻¹)
(b)
PTr
Clones
PTr to Clones
Clones to PTr
Ratios
P-5/P-6
P-4/P-5
P-3/P-4
P-2/P-3
P-1/P-2
Pp/P-1
(c)
PTr or Clones
PTr to Clones
Clones to PTr
Pupal weight (mg)
DiffSize (mg)

**Fig. 1.6.** (a) The relationship, for the northern experiment, between the difference in larval size at the onset of the ultimate instar and an estimated threshold size to pupate (DiffSize) and larval growth trajectories (GR), calculated as the observed growth rates during the 4th through the penultimate instar (calculated on logged mean replicate weights) . The linear regression line has been estimated after an ANCOVA determined there were no differences between feeding treatments. (b) Between-instar weight ratios for the four feeding treatments in the northern experiment (Ptr: quaking aspen [solid line]; clones [dashed-dotted line]; Ptr to clones [dashed line]; clones to Ptr [dotted line]). All ratios shown backwards relative to the pupal stage ($P_p/P_{-1}$: weight ratio between pupal weight and weight at the onset of the ultimate instar; $P_x/P_{x-1}$: weight ratio between weight at the onset of the X instar and weight at the onset of the X-1 instar. (c) Relationships between pupal weight and DiffSize. ANCOVA analysis determined that the intercept for the combined Ptr and clones treatments (solid line) was different from that of the Ptr to clones treatment (dashed line). There was no significant relationship for the clones to Ptr treatment (dotted line).

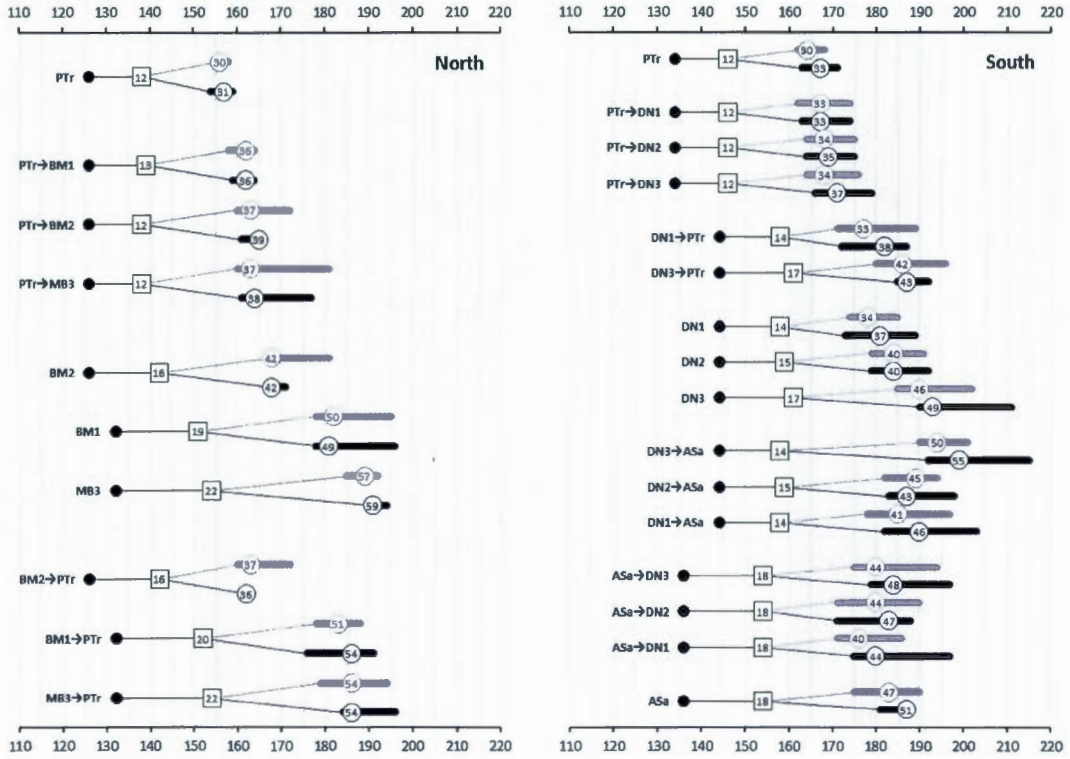



**Fig. 1.7.** Hosts and FTC phenologies in the northern and southern experiments: Julian day for larval hatch synchronized with budbreak (filled black circles) of quacking aspen (PTr), sugar maple (ASa), hybrid poplar northern clones (BM1, BM2 and MB3), and hybrid poplar southern clones (DN1, DN2 and DN3); Julian day for larvae to reach the 4$^{th}$ instar, when host switching was performed (empty squares; values within indicate the number of days since hatching); Julian day range for initiation of pupation (males: grey horizontal bars; females: black horizontal bars); Julian day to reach 50% of the larvae initiating pupation (empty circles; values within indicate the number of days since the 4$^{th}$ instar). Gray zones represent pupation ranges on aspen and sugar maple observed in other studies (see text for details). Note: all male larvae pupated the same day in the BM2 to PTr treatment.

**Table 1.** Results of multiple regression models on FTC pupal weight and time to pupation in the northern and the southern experiments using water and nitrogen contents of hosts foliage as independent variables.

| | | | | Water content (%) | | | | | Nitrogen content (%) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Experiment | Performance variable | Model | Sex | Estimate | SE | t ratio | p | partial $R^2$ | Estimate | SE | t ratio | p | partial $R^2$ | Model $R^2$ |
| Northern | pupal weight | Hosts | female | -48.50 | 22.32 | -2.17 | 0.053 | **0.73** | **312.23** | 90.28 | 3.46 | **0.005** | **0.81** | 0.87 |
| | | | male | -22.60‡ | 5.75 | -3.93 | **0.002** | **0.64** | **77.14‡** | 32.75 | 2.36 | **0.038** | 0.43 | 0.76 |
| | | Hosts + Switch | female | -17.01‡ | 4.54 | -3.74 | **<0.001** | 0.34 | **305.74‡** | 62.80 | 4.87 | **<0.001** | **0.45** | 0.62 |
| | | | male | -13.38‡ | 2.61 | -5.12 | **<0.001** | **0.49** | **90.27‡** | 36.05 | 2.50 | **0.017** | 0.23 | 0.57 |
| | time to pupation | Hosts | female | 7.75† | 1.27 | 6.12 | **<0.001** | 0.46 | **-67.88†** | 5.98 | -11.35 | **<0.001** | **0.81** | 0.96 |
| | | | male | 5.20† | 2.25 | 2.31 | **0.042** | 0.51 | **-55.24†** | 10.64 | -5.19 | **<0.001** | **0.79** | 0.86 |
| | | Hosts + Switch | female | 5.09† | 1.31 | 3.88 | **<0.001** | 0.52 | **-46.64†** | 6.25 | -7.46 | **<0.001** | **0.74** | 0.83 |
| | | | male | 2.98† | 1.50 | 1.99 | 0.055 | 0.56 | **-36.65†** | 7.17 | -5.11 | **<0.001** | **0.73** | 0.76 |
| Southern | pupal weight | Hosts | female | 22.37† | 5.26 | 4.25 | **0.001** | **0.59** | **129.47†** | 64.67 | 2.00 | 0.068 | 0.23 | 0.69 |
| | | | male | 12.50† | 3.02 | 4.14 | **0.001** | **0.57** | **84.53†** | 37.16 | 2.27 | **0.042** | 0.27 | 0.70 |
| | | Hosts + Switch | female | -9.02 | 7.23 | -1.25 | 0.219 | 0.02 | **253.56** | 89.65 | 2.83 | **0.007** | **0.14** | 0.17 |
| | | | male | -5.90 | 3.94 | -1.50 | 0.141 | 0.01 | **129.77** | 48.88 | 2.65 | **0.011** | **0.10** | 0.14 |
| | time to pupation | Hosts | female | **-2.05†** | 0.34 | -6.10 | **<0.001** | **0.58** | **-22.25†** | 4.12 | -5.40 | **<0.001** | **0.49** | 0.88 |
| | | | male | **-1.75†** | 0.25 | -7.09 | **<0.001** | **0.52** | **-24.38†** | 3.04 | -8.02 | **<0.001** | **0.61** | 0.92 |
| | | Hosts + Switch | female | **-1.70†** | 0.29 | -5.81 | **<0.001** | **0.43** | **-17.26†** | 3.37 | -5.12 | **<0.001** | **0.37** | 0.64 |
| | | | male | **-1.47†** | 0.25 | -5.80 | **<0.001** | **0.42** | **-16.91†** | 2.91 | -5.80 | **<0.001** | **0.42** | 0.67 |

†: averaged weighted means before the fourth instar, ‡: averaged weighted means after the fourth instar, no sign: weighted means averaged over the course of larval development. Estimate values in bold indicate sign in agreement with expectation. P-values in bold, indicate significant estimates. Partial R2 in bold indicate a dominant contribution to the model R2 by the variable, or equivalent contribution by the two variables.

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# CONCLUSION GÉNÉRALE

Cette étude avait pour but de déterminer la performance de la Livrée des forêts sur certains clones de peupliers hybrides recommandés pour les différentes régions du nord et du sud du Québec relativement à ses hôtes naturels, le peuplier faux-tremble et l'érable à sucre. Elle visait aussi à évaluer la performance de l'insecte dans un contexte de migration entre hôtes naturels et plantations de peupliers hybrides afin d'être en mesure de connaître les risques associées à une proximité des plantations et des hôtes naturels.

Il a été mis en évidence que les clones du nord étaient résistants à la Livrée des forêts relativement au peuplier faux-tremble. Dans le cas des clones du sud, une performance intermédiaire a été observée pour la livrée car la performance des larves sur ces hôtes était à peine plus faible que sur le peuplier faux-tremble, et légèrement supérieure à celle observée sur l'érable à sucre. Dans une situation de migration de l'insecte du peuplier faux-tremble vers les clones, autant du nord que du sud, malgré un faible poids de chrysalide, les larves se sont développées rapidement et ont eu un meilleur taux de survie que sur les clones. Par rapport à l'érable à sucre, la performance des larves sur les clones du sud a été peu affectée, même que le taux de survie était supérieur sur les clones que sur l'érable. Il y avait peu de variations dans la performance des larves ayant migré de l'érable à sucre vers les clones du sud. Par contre, la performance des larves sur l'érable à sucre et les clones du sud restent inférieure à celle sur le peuplier faux-tremble. Le temps de développement est la variable de performance qui est systématiquement la plus affectée par la qualité des diètes.

En regard des deux hypothèses posées à l'initiation de ce projet de recherche (**H1 :** la performance est intermédiaire lorsque les larves se nourrissent de deux hôtes de

différentes qualité et **H2 :** la performance globale est meilleure lorsque le premier hôte est de meilleure qualité ), les résultats obtenus les confirment et elles peuvent donc servir à prédire les performances de la Livrée des forêts en situation de changement de diète (e.g., hôte naturel vers clones) dans les cas où l'antixénose des clones n'est pas prononcée ou maintenue durant la saison de croissance. Cependant, cette étude a permis de confirmer également, et de mettre en évidence, les contraintes développementales propres à la Livrée des forêts. Ces contraintes, révélées dans l'étude d'Étilé et Despland (2008), concernent l'existence d'un poids seuil critique que les larves doivent franchir pour accomplir un dernier stade larvaire et la métamorphose pupale qui s'en suit. Les conséquences sont un prolongement du temps de développement larvaire par ajout de stades. Ainsi, la réponse de la livrée à la résistance des clones de peuplier hybrides se traduit par un déphasage dans le temps de l'émergence des adultes, ce qui entraînerait une ségrégation reproductive et augmenterait les risques de développement rapide de biotypes adaptés aux clones résistants.

Les peupliers naturels sont des essences très abondantes au Québec et au travers l'Amérique du Nord. Le développement d'une production d'arbres à croissance rapide tels que les peupliers hybrides, qui sont aussi des croisements du genre *Populus*, dans cette matrice de peupliers naturels, imposent aux peupliers hybrides les contraintes des ravageurs des peupliers. La Livrée des forêts, en tant que plus important défoliateur des peupliers ne fait pas exception. D'autres lépidoptères sont aussi ciblés comme défoliateurs potentiels des peupliers hybrides, soit la tordeuse du tremble (*Choristoneura conflictana* Walker) et la spongieuse (*Lymantria dispar* L.). Au Canada on retrouve la tordeuse du tremble à peu près partout où l'on trouve du peuplier faux-tremble. C'est un insecte printanier souvent associé aux phases d'infestations de la Livrée des forêts.

Contrairement à la livrée, la chenille de la tordeuse du tremble est très peu mobile, et aux stades avancés, elle s'enroule dans les feuilles pour se protéger et s'alimenter (Cerezke, 1992). Hormis en période épidémique, les plantations de peupliers hybrides pourraient jouir d'un plus grand isolement des populations de cette tordeuse présente dans les réservoirs que sont les forêts naturelles de peuplier faux-tremble. On retrouve la spongieuse au Québec et en Ontario ainsi que dans le nord-est et le centre nord des États-Unis. À l'inverse de la livrée, cet insecte s'alimente une fois adulte, sa fenêtre de possibilité pour la reproduction est donc plus large (Humble et Stewart, 1994). Il y a aussi le coléoptère *Chrysomela scripta* (F.) qui est un important ravageur des peupliers. Il s'alimente surtout dans les jeunes tiges et dans les jeunes plantations. Cette espèce a par contre une biologie tout autre que la Livrée des forêts. *C. scripta* fait généralement plus d'une génération par année (Bingaman & Hart, 1992) et comme il s'alimente une fois adulte, sa fenêtre pour la reproduction est plus grande et il pourra y avoir plus facilement une dilution des gènes de résistance.

On retrouve dans la littérature, ce de manière récurrente, qu'il est nécessaire de déployer plusieurs clones au sein d'une même plantation. Cette proposition de plantations polyclonales semble reposer sur deux approches de gestion ayant été développées dans deux buts très différents. La première est plutôt dans l'optique d'éviter le plus possible les risques de pertes engendrées par des ravageurs (et même les risques associés aux perturbations abiotiques) et maintenir une productivité élevée de la plantation. En ayant des clones de peupliers hybrides avec divers degrés de résistance, les arbres ne sont pas tous autant attaqués, ce qui permet de conserver un certain rendement (Coyle et al., 2002; Hühn, 1986). Le fonctionnement de cette approche reste à démontrer, car ceci impliquerait la mise en place de dizaines de clones simultanément, adaptés aux conditions locales des plantations. La deuxième approche, traitée par Gould (1983) pour les systèmes agricoles, a pour but d'éviter l'apparition de biotypes résistants chez les insectes ravageurs. L'utilisation de clones plus susceptibles aux insectes parmi des clones résistants permet la reproduction

d'individus ayant développé une contre-résistance avec des individus non-résistants. De cette façon, le développement d'une contre-résistance est minimisé ou ralenti (Hurley et al., 1997; Raffa, 1989; Gould, 1991). Les contraintes de développement chez la Livrée des forêts, qui entraînent un prolongement de son temps de développement, de même que sa courte durée de vie adulte, comme elle ne s'alimente pas, amènent une réflexion sur ces stratégies de déploiement de plantations polyclonales. Ceci amène à se poser la question si cela ne faciliterait pas, au contraire, le développement plus rapide d'une contre-résistance chez la Livrée des forêts. En revanche, le déploiement de différents clones résistants au sein d'une même plantation pourrait théoriquement permettre aux livrées de se reproduire entre elles si les fenêtres de reproduction sont les mêmes sur les différents clones. Si les facteurs de résistance chez ces clones concernent des gènes différents chez la livrée, alors il y a lieu de penser qu'une telle stratégie serait plus stable dans le temps que de déployer des clones avec des degrés de résistance différents (Coyle et al., 2002; Roberds et Bishir, 1997; Robison, 2002).

# ANNEXE

## Liste des articles publiés sur les relations insectes-peupliers hybrides

| Auteurs | Ordre | Espèce | Performance | Préférence | Susceptibilité des clones |
|---|---|---|---|---|---|
| Alfaro-Tapia et al., 2007 | Homoptère | *Chaitophorus leucomelia* | X | | |
| Bingaman & Hart, 1992 | Coléoptère | *Chrysomela scripta* | | X | |
| Broberg & Borden, 2005 | Coléoptère | *Cryptorhynchus lapathi* | X | X | |
| Broberg et al., 2005 | Coléoptère | *Cryptorhynchus lapathi* | | X | |
| Broderick et al., 2010 | Lépidoptère | *Lymantria dispar* | X | | |
| Brown et al., 2006 | Lépidoptère | *Paranthrene robiniae* | | | X |
| Hannon et al., 2008 | Coléoptère | *Cryptorhynchus lapathi* | X | | |
| Harrel et al., 1981 | Coléoptère | *Chrysomela scripta* | | X | |
| Johnson & Johnson, 2003 | Coléoptère | *Cryptorhynchus lapathi* | | | X |
| Kleiner et al., 1998 | Lépidoptère | *Lymantria dispar* | X | | |
| Kruse & Raffa, 1996 | Lépidoptère | *Lymantria dispar* | X | | |
| Kruse & Raffa, 1997 | Lépidoptère | *Lymantria dispar* | X | | |
| La Spina et al., 2010 | Coléoptère | *Chrysomela populi* | X | | |
| Labrecque & Teodorescu, 2005 | NA | NA | | | X |
| Lindroth et al., 1993a | Lépidoptère | *Lymantria dispar* | X | | |
| Lindroth et al., 1993b | Lépidoptère | *Lymantria dispar* | X | | |
| Nordman et al., 2005 | Coléoptère<br>Lépidoptère<br>Diptère | 7 espèces | | X | |
| Pearson et al., 2010 | NA | NA | | | X |
| Ramirez et al., 2004 | Homoptère | *Chaitophorus leucomelia* | X | | X |
| Robison & Raffa, 1994 | Lépidoptère | *Malacosoma disstria* | X | X | |
| Robison & Raffa, 1997 | Lépidoptère | *Malacosoma disstria* | X | X | |
| Robison & Raffa | Coléoptère | *Chrysomela scripta* | | | X |
| Tharakan et al. | NA | NA | | | X |
| Tomescu & Nef | NA | NA | | | X |

**Liste bibliographique des articles publiés sur les relations insectes-peupliers hybrides (Tableau 2)**

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